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Description of the immature stages and life history of *Euselasia* (Lepidoptera: Riodinidae) on *Miconia* (Melastomataceae) in Costa Rica

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Abstract

The immature stages and life histories of *Euselasia chrysippe* (Bates, 1866) and *E. bettina* (Hewitson, 1869) are described, providing the first detailed morphological characters for the subfamily Euselasiinae. The larvae of *Euselasia chrysippe* and *E. bettina* specialize on several species of *Miconia* (Melastomataceae). The eggs are stalked (the first reported case of such in Lepidoptera) and laid in clusters on the underside of leaves. The larvae are gregarious and feed, rest, molt, and pupate 'synchronously'. Both species have six larval instars which exhibit processionary behavior throughout their development. SD2 setae on the prothoracic shield are sensitive to airborne vibrations and are related to the head-flicking behavior exhibited by larvae while feeding, perhaps as a defensive strategy to deter attacks by parasitoids. Several morphological characters of first instar larvae are unique among Lepidoptera: extra setae, bifurcated dorsal setae on A1–8, and various organs. Sixth instar larvae possess subcircular plates on the dorsolateral surfaces of all segments of the thorax and abdomen. These smooth plates have a metallic-blue iridescence that is structural in nature. Pupation occurred singly or gregariously under laboratory conditions. The total duration of the life cycle under laboratory conditions lasted up to eight weeks. New records of parasitoids for *Euselasia* include *Encarsia* and *Telenomus* from eggs. A list of host plants recorded for Euselasiinae, a summary of parasitoid records for *Euselasia*, and summary tables of unique organs and setae of immature stages are provided. *Euselasia chrysippe* and *E. bettina* are currently considered potential biocontrol agents for *Miconia calvescens* DC in Hawaii.

Key words: auditory mechanoreceptor, biological control of weeds, metalmark butterflies, *Calolydella*, *Corrachia*, *Encarsia*, *Euselasia aurantia*, *E. bettina*, *E. chrysippe*, gregarious, host plants, *Miconia calvescens*, Nemeobiinae, Neotropical, processionary behavior, structural color, *Telenomus*

Resumen

Se describe en detalle las historias naturales y los estadios inmaduros de *Euselasia chrysippe* (Bates, 1866) y *E. bettina* (Hewitson, 1869), brindando por primera vez caracteres morfológicos en detalle para la subfamilia Euselasiinae. Las larvas se especializan en especies de *Miconia* (Melastomataceae). Los huevos son sostenidos por un pedúnculo (el primer caso que se encuentra de esta condición en Lepidóptera) y son puestos en grupos en el lado inferior de las hojas. Las larvas son gregarias y se alimentan, descansan, mudan y pupan 'sincronizadamente'. Ambas especies pasan por seis estadios larvales y muestran comportamiento procesionario a través de su desarrollo. Las setas SD2 en la placa del protórax son sensibles a vibraciones del aire, y están relacionadas con el comportamiento de tiritar de cabeza de las larvas mientras se alimentan, probablemente parte de una estrategia defensiva para detener ataques de parasitoides. Los caracteres morfológicos de la larva en el primer estadio son únicos entre Lepidoptera por tener un número extra de setas, setas dorsales bifurcadas en A1–8 y varios otros órganos. La larva del sexto estadio posee placas sub-circulares en la superficie dorso-lateral de todos los segmentos del tórax y abdomen. Estas placas lizas producen una iridiscencia azul metálica que es estructural en la naturaleza. La pupación se dio individualmente o de forma gregaria. La duración total del ciclo de vida bajo condiciones de laboratorio se extendió hasta ocho semanas. Nuevos registros de parasitoides para *Euselasia* incluyen *Encarsia* y *Telenomus* a partir de huevos. Se presenta una lista de plantas hospederas registradas para la súbfamilia Euselasiinae, un resumen de parasitoides registrados para *Euselasia* y cuadros resumidos de órganos y setas de estadios inmaduros. Estos dos riodínidos son actualmente considerados como potenciales agentes de control biológico para *Miconia calvescens* DC. en Hawai.

Palabras clave: *Calolydella*, color estructural, comportamiento de procesión, control biológico de malezas, *Encarsia*, *Euselasia aurantia*, *E. bettina*, *E. chrysippe*, gregario, mariposas diurnas, plantas hospederas, mecanoreceptor auditorio, *Miconia calvescens*, neotrópico, Nemeobiinae, *Telenomus*

Introduction

For more than 50 years *Miconia calvescens* DC. (Melastomataceae) has had a negative impact on the native ecosystems of several oceanic islands (Vitousek *et al.* 1997). It is one of the most invasive plants in the Pacific and has been considered one of the world's most threatening noxious weeds since 1992 (Conant *et al.* 1997; ISSG 2005; PIER 1999–2006). Loope & Helweg (2004) report that more than $1,000,000 US is spent yearly to protect native biodiversity on the island of Maui alone. In addition to mechanical and chemical controls, biological control of *M. calvescens* is important and necessary (Medeiros & Loope 1997). During a search for biological control agents against *M. calvescens* in Costa Rica, where the plant is native, immature stages of two species of *Euselasia* Hübner, [1819] (Lepidoptera: Riodinidae: Euselasiinae) were found: *E. chrysippe* (Bates, 1866) and *E. bettina* (Hewitson, 1869). They were targeted as possible biocontrol agents for *M. calvescens*, and thus their biologies were studied in detail.

The subfamily Euselasiinae Kirby 1871 (1867) is restricted to the Neotropics and contains three tribes: Stygini, Corrachiini, and Euselasiini. Stygini and Corrachiini are each monotypic, consisting of *Styx infernalis* Staudinger, 1876 and *Corrachia leucoplaga* Schaus, 1913, respectively (Callaghan & Lamas 2004). The tribe Euselasiini contains three genera: *Methone* Doubleday, *Hades* Westwood, and *Euselasia*. The first two genera contain only one (*M. cecillia* (Cramer, 1777)) and two species (*H. noctula* Westwood, 1851; *H. hecamode* Hewitson, 1870), respectively (Callaghan & Lamas 2004). In contrast, *Euselasia* contains approximately 170 described species (Stichel 1930–1931; Hall & Willmott 1998; Callaghan & Lamas 2004; Hall & Willmott 2009) making it the largest genus in the family. The closely related subfamily Nemeobiinae is found in the Old World (Oates & Emmet 1990; Corbet & Pendlebury 1992; Samson *et al.* 1999; Braby 2000, 2004; Wahlberg 2005).

Despite the large number of species, the biology and immature stages of the genus *Euselasia* are poorly known (D.J. Harvey & J.P.W. Hall, pers. comm. 2006). Although the life history of some pest species on *Eucalyptus* and other myrtaceous species are relatively well studied, most information comes from brief notes in literature published over the past 200 years (see Table 1 for references). Rearing data of ten species of *Euselasia* and *Hades noctula* from northwestern Costa Rica are provided by Janzen & Hallwachs (2009).

All of the records above, including that of Stygini (Lamas 2003) and Corrachiini (K. Nishida, in prep.) indicate that larvae are gregarious and most likely processionary, social (Costa & Fitzgerald 1996, 2005; Fitzgerald 2005a; Costa 2006). The morphology of the early stages of *Euselasia* has been studied by Harvey (1987a, 1987b, 1989) and eggs of *E. hieronymi* are illustrated and described by Downey and Allyn (1980). Demography of *E. chrysippe* on *M. calvescens* was studied by Allen (2007).

Species of *Euselasia* occur between southwestern North America (Mexico) and the tropical regions of South America (Northern Argentina) with greatest diversity in the Amazon Basin (DeVries 1997; Funet 2005–2007). Many new *Euselasia* species have been discovered recently (Hall & Willmott 1998; Hall & Lamas 2001; Hall & Willmott 2009; Janzen & Hallwachs 2009; I. Nakamura, pers. comm. 2006), with approximately 30 species recorded from Costa Rica (DeVries 1997; Janzen & Hallwachs 2009). Most species are restricted to specific habitats and hence are rare in collections (DeVries 1997). Host plant families recorded for the genus include Clusiaceae, Euphorbiaceae, Melastomataceae, Myrtaceae, Sapotaceae, and Vochysiaceae (Table 1). Previously reported records of parasitoids of *Euselasia* species include the families Chalcididae, Ichneumonidae, Trichogrammatidae (Hymenoptera), and Tachinidae (Diptera) (Table 2).

Euselasia chrysippe (Figs. 1–3, 6–8) is recorded from southeastern Mexico to northern Colombia (DeVries 1997; NABA 2004; Warren *et al.* 2005). Currently this species is being reared in quarantine in Hawaii for the biological control of *Miconia calvescens* (T. Johnson, pers. comm.). It ranges throughout Costa Rica from sea level along the Atlantic lowlands (e.g., Cahuita and Tortuguero) to approximately 1500 m along the Northern and Central Volcanic Cordillera and in the Central Pacific Regions (DeVries 1997; INBio 1997–2006; Chacón 2001; Janzen & Hallwachs 2009). Flight activities and immature stages are briefly described by DeVries (1997). Previously reported host plants for *E. chrysippe* include *Miconia calvescens*, *M. elata* (Sw.) DC., *M. trinervia* (Sw.) D. Don ex Loud., *Conostegia rufescens* Naudin, all Melastomataceae, and one other undetermined melastome species (Table 1). Adults have been observed visiting sticky buds of *Ficus*

(Moraceae) and extrafloral nectaries of *Inga* (Fabaceae) and *Passiflora* (Passifloraceae) (DeVries 1997). Natural enemies recorded for *E. chrysippe* include parasitoids (Table 2), undetermined ants predating on egg masses, Reduviidae on recently hatched larvae, Salticidae on mid-instar larvae, and a *Polybia* sp. (Vespidae) on the last instar larva (Allen 2007).

Little is known about *Euselasia bettina* (Figs. 4–5, 9–10). It occurs from Nicaragua to Ecuador and has been collected between 400 and 1250 m elevation on both the Atlantic and Pacific slopes in Costa Rica (DeVries 1997; INBio 1997–2006; personal observation). DeVries (1997) described flight activities of the adults. The host plant and early stages have not been reported previously.

Cryptic species are prevalent in *Euselasia* (DeVries 1997; J.P.W. Hall, pers. comm.). Therefore, careful observations with detailed descriptions and illustrations in addition to molecular analyses are suggested for future studies of the genus. In this paper, the life histories and morphology of immature stages of *E. chrysippe* and *E. bettina* are described, illustrated in detail, and diagnosed, representing the first descriptions of the early stages of Euselasiinae. General morphological descriptions of the adult and detailed studies on the life history are provided for field use by biological control workers. A list of host plants recorded for the subfamily Euselasiinae, a summary of parasitoid records, and unique organs and setae of *Euselasia* are also supplied.

Materials and methods

Study sites. Other than a brief study in 2007–2008, the field study was mostly conducted from September 2000 to December 2003 in primary and secondary forests in Costa Rica, mainly along roadsides at the following sites: Laguna de Hule (elevation 700–800 m; 1018'15"N, 8412'23"W) (Figs. 11, 51), El Ángel-Cariblanco (750 m; 1015'44.2"N, 8410'19.4"W), and Estación Biológica La Selva of the Organization for Tropical Studies (OTS), Puerto Viejo de Sarapiquí (30 m; 1012'38.6"N, 8340'45.6"W) in Heredia Province; the north side of Lake Arenal (500–550 m; 1028'17"N, 08446'11"W) in Alajuela and Guanacaste provinces; Hitoy Cerere Biological Preserve (100 m; 0940'19"N, 8301'28"W) in Limón Province; and Jicotea, Turrialba (Figs. 12–15) (900 m, 0948'29.3"N, 08331'23.0"W) in Cartago Province. All of these sites are on the Atlantic slope in the Tropical Temperate Humid Forest life zone which has no dry season (Herrera S. & Gómez P. 1993). A brief study involving the release of adults was conducted in Reserva Ecológica Leonelo Oviedo on the campus of Universidad de Costa Rica (UCR) (1160 m; 0956'15"N, 08403'00"W) (Nishida *et al.* 2009).

Host plant. *Miconia calvescens* occurs naturally from southern Mexico to Central America, extending into South America to northern Argentina and southern Brazil (Missouri Botanical Garden 2005). The species was introduced to the main island of Tahiti from Central America in 1937 as an ornamental in a botanical garden (Meyer & Florence 1996). Today the plant has displaced more than 70% of the Tahitian native forest—vast monospecific stands of *M. calvescens* extend across the island's mountain hillsides (Binggeli 1998; PIER 1999–2006). It became established in the Hawaiian Islands after its introduction in 1961 (Medeiros & Loope 1997). Recently, *M. calvescens* became established in Queensland, Australia, and French Polynesia, and it also is reported in Jamaica and Sri Lanka (Csurhes & Edwards 1998; GISP 2003). In Costa Rica, the plant occurs between 100 and 900 m elevations on the Atlantic slope (Proyecto Miconia UCR, unpublished). Two color forms of leaves are found in Costa Rica: in one form they are entirely green and in the other they are purple on the underside. Mature leaves usually are between 35 and 55 cm long. The underside of the leaf surface has loosely scattered minute brown stellate (starlike) trichomes along the veins (Figs. 19, 52–54, 78) and fine, ca. 0.5 mm long translucent or black hairlike trichomes (Fig. 78). In the Neotrops *Miconia* species are pollinated by various types of bees (Renner 1989). The berrylike fruit contains 100–200 small seeds (Meyer 1998; PMIS 2002) and a prolific tree can bear millions of fruits (Hawaii Department of Land & Natural Resources 1996) which are dispersed primarily by birds (Medeiros & Loope 1997, and references therein). In the Ecological Preserve on UCR campus there are approximately 15 plants 0.5–2.5 m tall (planted mid-2003) and 10 plants 0.5–1.0 m tall (planted in late 2002) (Allen 2007).

Life history and experiments. Leaves of *Miconia calvescens* on small saplings (approximately 0.3 m tall with stem diameter <0.5 cm at the base) and a few cut-off branches of large trees (ca. 6.0 to 8.0 m tall with 10 to 15 cm trunk diameter) were examined thoroughly in the field. Small pieces of leaves with eggs or early

instar larvae were cut out and placed in plastic vials. Mid- to late-instar larvae were placed in transparent plastic bags, along with entire leaves, for transport and rearing in the laboratory at ca. 23.5–24.5 °C daily average. Temperature in the field was measured by a Casio Protrek watch (model PRG-70J) placed near the plants. Under rearing conditions, eggs were checked and exposed to fresh air frequently to minimize fungal growth. When fungal growth was detected on eggs, it was removed with a dry, fine-hair brush. After hatching from eggs, larvae were transferred onto a fresh leaf using a soft brush, or the cut-out leaves with the larvae were stapled onto potted plant leaves. The potted plants were between 30 and 60 cm tall; stem base diameter was less than 5.0 mm. The plants usually had 4 to 6 small leaves, 15 to 25 cm long and 8.0 to 13 cm wide. The flower pots were partially submerged in water to prevent the escape of the larvae. Some larvae were reared in transparent plastic bags. Fresh leaves or new potted plants were supplied when all the leaves of a plant had been used. Pupae were placed and reared in an acrylic chamber approximately 50 cm tall, 80 cm wide, and 60 cm deep with a clear translucent front in which the humidity was kept high with frequent spraying of distilled water. Subsets of eggs, larvae of each instar, head capsules of each instar, and pupae were preserved in 75–80% EtOH. Only a few eclosed adults were pinned and spread. The majority of adults were kept alive in the chamber and fed rotten banana (Bauerfeind & Fischer 2005), guava fruit, and distilled water drops. A weak solution of honey-water (less than 25%) (Braby & Jones 1995; O'Brien *et al.* 2005) was sprayed on leaves or the chamber surface until adults were released near planted *Miconia calvescens* in the Ecological Preserve on the UCR campus.

One to two day-old females (n = 21) and males (n = 19) consisted of two groups of *E. chrysippe* reared from eggs collected from the Lake Arenal site which were released at the Albergue La Catarata Butterfly Garden in La Fortuna de San Carlos near Lake Arenal in mid-December 2003. The butterfly garden is enclosed with black-meshed netting. The tallest roof area was ca. 3.5 m and the lowest was ca. 2.0 m from the ground. Butterflies were released at 1700 hours and courtship behavior was observed the next morning between 0630 and 0730.

Most of the preliminary observations and experiments of processionary behavior were conducted on flower pot rims using mature last instar larvae of both *E. chrysippe* and *E. bettina* searching for pupate sites; they were digitally video-recorded. For a closer examination of the ventral part of the larvae in motion, a group of last instar *E. chrysippe* larvae moving in procession were placed in a transparent plastic bag and observed under a stereo-microscope (32x).

While rearing larvae, an auditory response, possibly representing a defensive behavior, was observed in both species. After careful examination of the larval morphology, it was discovered that the pair of SD2 setae on the prothoracic shield are distinct from other setae and appeared to be sensitive to air movement (see results). These observations raised several questions: Are the SD2 setae sensitive to airborne vibrations? Do they have an auditory function? Is the auditory-responding 'defensive' behavior triggered by airborne vibrations via the SD2 setae? The questions led to the hypothesis that larvae without SD2 setae will not respond to airborne vibration and therefore will not show the 'defensive' behavior. Experiments conducted briefly in 2007 are as follows. A group of 50 last instar *Euselasia chrysippe* larvae was collected at Estación Biológica La Selva. An auditory stimulus, violin pizzicato at frequencies between approximately 196 and 700 Hz, was given while the larvae fed on leaves. The choice of instrument was determined by convenience; i.e., the author had available to him a standard four-string violin. The sound frequency (units of cycles per seconds/Hz) followed the fundamental frequency piano table (e.g., in Mathematical Harmonies 2007). After a preliminary experiment, the 'A' string (440.00 Hz) was selected as the experimental frequency. SD2 setae were removed from the prothoracic shield by pulling them out using forceps while the larvae were feeding on leaves. Of the 50 larvae, ten were randomly selected and the SD2 setae were removed. Fourteen untreated larvae were randomly selected and placed with the ten treated larvae. The 24 larvae were divided into four groups of six larvae and were observed under the stereo-microscope while they fed on leaves. Each group was exposed to 10 'strong' pizzicato plucks of the 'A' string every other second, approximately 15 cm away from the larvae, with the upper surface of the violin facing the larval dorsum.

Another experiment was conducted to determine the cause of color differences among pupae. Most of the pupae reared in transparent plastic bags were much paler than those that pupated in darker locations. Thus,

two sets of 16 recently prepupated (silk strand-spun) larvae (n = 1 group) in plastic bags were placed in a dark environment (in three layers of black plastic bags). One group was removed from the black plastic bags after ca. eight hours and exposed to intense indirect sunlight. The other was kept in the black plastic bags for 32 hours.

Immature stages. Most of the observations were made during 2005–2006. More than three groups of live specimens of each stage of both species were observed and photographed to document general appearance. Preserved specimens of immature stages were examined using a dissecting stereo-microscope (8–64X) and a scanning electron microscope (SEM). Approximate measurements and ratios of measurements of first instar larvae were obtained using SEM images. For SEM study, specimens were first hydrated, cleaned using a soft brush, and allowed to sit in 100% 409 detergent (Clorox Company of Oakland, California, USA) for 15–20 minutes. After preliminary dehydration in a series to 100% EtOH, specimens were further dehydrated in liquid CO_2 using a Balzers CPD030 critical point dryer. Specimens were coated with gold palladium using a Cressington 108A sputter coater. Most of the images were obtained using an Amray 1810 electron microscope with LaB6 filament at an acceleration voltage of 10 kV. A few images were obtained using a Leica Steroscan 440 LaB6. Terminology for structures of the egg follows Downey & Allyn (1980) and DeVries (1997); terminology for larval features follows Hinton (1946), Stehr (1987), Albert (1980), Duarte *et al.* (2005), and Landry *et al.* (2006); and terminology for pupae follows Mosher (1916) and Patočka & Turčáni (2005). Several new terms are used and applied to previously unknown organs and setae.

General. In many instances, images of *Euselasia bettina* are used to show overlapping data or characters of *E. chrysippe*. The term 'group' is used herein instead of 'cohort' since the larvae of two cohorts or more can merge together and make a single group. High resolution (3 mega pixels or higher) digital photographs were taken by Nikon Coolpix cameras (models E990 and E4500). Short, low resolution digital videos were recorded in QuickTime Movie (.MOV) format (2006 Apple Computer, Inc.) using the Coolpix cameras. All digital images were processed with Adobe Photoshop. Video recordings of processionary behavior, preliminary experiments on larval and pupal behaviors, and other aspects of life history are posted on the Internet (Fitzgerald 2005b; Nishida 2007). Sample sizes indicated by '(n = ca.)' are estimated numbers without precise records. Voucher specimens are deposited in the United States National Museum, Washington D.C.; Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; and the Entomological collections of the Museo de Zoología, Escuela de Biología, UCR. Nomenclature and scientific names of butterflies follow Wahlberg *et al.* (2005) and Callaghan & Lamas (2004), except for *Euselasia cheles* (Godman & Salvin, 1889) (Janzen & Hallwachs 2009). Bibliographical information of butterfly species was obtained from Lamas *et al.* (1995) and Lamas (2007). Missouri Botanical Garden (2005) was consulted for the scientific names of plants.

Acronyms, abbreviations, and numerical nomenclature. The following are used in the text and/or figures: 1 = sensilla basiconica, 2 = sensillum chaetica, 3 = sensillum styloconicum, 4 = sensillum trichodeum (in antennal sensilla); A1, A3 = apical sensilla basiconica, A2 = apical sensillum styloconicum, L1–3 = lateral sensilla basiconica, M1–2 = medial sensillum basiconica, SD = sensillum digitiform (in sensilla of maxillary palpus); A = abdomen; ACG = área de conservación Guanacaste; AF = adfrontal seta, AFa = adfrontal pore; AHS = arrowhead setae; An = antenna; At = anterior seta; ATP = anterior tentorial pit; BLS = bladelike seta; C = clypeal seta; CBS = clubbed seta; Cl = clypeus; CO = cupola organ; CS = claw-shaped setae; CTO = circular tablet organ; cx = cervix; cxa = coxa; D = dorsal seta; Da = dorsal pore; E = eye piece; F = frontal seta; Fa = frontal pore; FS = flat seta; L = lateral seta; LA = lateral seta on labrum; Li = labium; Lr = labrum; M = medial seta; Ma = mandible; MD = microdorsal; MDa = microdorsal pore; ML = mesothoracic leg; MP = maxillary palpus; Mx = maxilla; P = posteriodorsal seta; PCO = perforated cupola organ; pl = proleg; PL = prothoracic leg; "PP" = "proprioceptor" seta; PPO = perforated plate organ; Pr = proboscis; S = stemmatal seta; SC = silk clipper; SCS = stalk conjunctional structure; SD = subdorsal seta; SO = spherical organ; sp = spiracle; SR = spinneret; SS = substemmatal seta; STS = spatulate-tipped setae; SV = subventral seta; T = thorax; Tsp = thoracic spiracle; tz = subdorsal triangular zone; V = ventral seta; W = wing sclerite; XD = primary seta.

TABLE 1. List of host plants recorded for the subfamily Euselasiinae. All data of personal communication and personal observations are based on rearing of immature stages. Undetermined plant species' data from Janzen & Hallwachs as cited in Janzen & Hallwachs (2009).

Butterfly species [note]	Author(s) and year	Host plant family	Host plant species and author [note]	Locality	Source
Styx					
Styx infernalis	Staudinger, 1876	Myrsinaceae	*Myrsine* sp.	Peru	Lamas 2003
Corrachia					
Corrachia leucoplaga	Schaus, 1913	Myrsinaceae	*Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult.	Costa Rica	K. Nishida pers. obs. 2009*
Hades					
Hades hecamede	Hewitson 1870	Clusiaceae	*Clusia* sp.	Colombia	Beccaloni *et al.* 2008
Hades noctula	Westwood, 1851	Anacardiaceae	*Anacardium excelsum* (Kunth) Skeels	Costa Rica	Janzen & Hallwachs 2009
Hades noctula	Westwood, 1851	Anacardiaceae	*Rhus striata* Ruiz & Pav.	Colombia	Beccaloni *et al.* 2008
Hades noctula	Westwood, 1851	Anacardiaceae	*Spondias mombin* L.	Costa Rica	DeVries 1997
Hades noctula	Westwood, 1851	Anacardiaceae	*Spondias mombin* L.	Costa Rica	Janzen & Hallwachs 2009
Hades noctula	Westwood, 1851	Anacardiaceae	*Spondias mombin* L.	Costa Rica	Janzen & Hallwachs 2009
Hades noctula	Westwood, 1851	Anacardiaceae	*Spondias mombin* L.	Costa Rica	Harvey 1987a
Hades noctula	Westwood, 1851	Anacardiaceae	*Spondias mombin* L.	Central America	Harvey 1987b
Hades noctula	Westwood, 1851	Anacardiaceae	*Tapirira mexicana* Marchand	Costa Rica	Janzen & Hallwachs 2009
Euselasia					
Euselasia arcana	Brévignon 1995	Clusiaceae	*Clusia* sp.	French Guiana	Brévignon 1995
Euselasia amphidecta	(Godman & Salvin, 1878)	Euphorbiaceae	*Hieronyma oblonga* (Tul.) Müll. Arg.	Costa Rica	Janzen & Hallwachs 2009
Euselasia aurantia	(Butler & H. Druce, 1872)	Melastomataceae	*Miconia appendiculata* Triana	Costa Rica	K. Nishida, pers. obs. 2006
Euselasia aurantia	(Butler & H. Druce, 1872)	Melastomataceae	*Miconia calvescens* Schrank & Mart. ex DC.	Costa Rica	Proyecto Miconia UCR, unpublished
Euselasia aurantia	(Butler & H. Druce, 1872)	Melastomataceae	*Miconia schlimii* Triana	Costa Rica	Eduardo Chacón-Madrigal, pers. comm. 2007
Euselasia aurantiaca	(Salvin & Godman, 1868)	Clusiaceae	*Clusia* sp.	Central America	Harvey 1987b
Euselasia bettina	(Hewitson, 1869)	Melastomatacee	*Miconia calvescens* Schrank & Mart. ex DC.	Costa Rica	Proyecto Miconia UCR, unpublished
Euselasia bettina	(Hewitson, 1869)	Melastomatacee	*Miconia theaezans* (Bonpl.) Cogn.	Costa Rica	Eduardo Chacón-Madrigal, pers. comm. 2005
Euselasia nr. *cafusa*	----------	Myrtaceae	*Eugenia* sp.	Costa Rica	DeVries *et al.* 1994
Euselasia cheles	(Godman & Salvin, 1889)	Clusiaceae	*Clusia cylindrica* Hammel	Costa Rica	Janzen & Hallwachs 2009
Euselasia cheles	(Godman & Salvin, 1889)	Clusiaceae	*Clusia minor* L.	Costa Rica	Janzen & Hallwachs 2009
Euselasia cheles	(Godman & Salvin, 1889)	Clusiaceae	*Clusia quadrangula* Bartlett	Costa Rica	Janzen & Hallwachs 2009
Euselasia cheles	(Godman & Salvin, 1889)	Clusiaceae	*Clusia* sp.	Costa Rica	K. Nishida pers. obs. 2002

TABLE 1. (continued)

Butterfly species [note]	Author(s) and year	Host plant family	Host plant species and author [note]	Locality	Source
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Conostegia rufescens* Naudin	Costa Rica	Janzen & Hallwachs 2009
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia appendiculata* Triana	Costa Rica	Eduardo Chacón-Madrigal, pers. comm. 2007
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia calvescens* Schrank & Mart. ex DC.	Costa Rica	DeVries 1997
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia calvescens* Schrank & Mart. ex DC.	Costa Rica	Proyecto Miconia UCR, unpublished
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia donaeana* Naudin	Costa Rica	Eduardo Chacón-Madrigal, pers. comm. 2005
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia elata* (Sw.) DC.	Costa Rica	DeVries *et al.* 1994
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia impetiolaris* (Sw.) D. Don ex DC.	Costa Rica	K. Nishida, pers. obs. 2007
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia longifolia* (Aubl.) DC.	Costa Rica	Eduardo Chacón-Madrigal, pers. comm. 2007
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	*Miconia trinervia* D. Don ex G. Don	Costa Rica	Janzen & Hallwachs 2009
Euselasia chrysippe	(H. W. Bates, 1866)	Melastomataceae	Janzen & Hallwachs, see description	Costa Rica	Janzen & Hallwachs 2009
Euselasia euboea	(Hewitson, [1853])	Myrtaceae	*Eugenia uniflora* L.	Brazil	Silva *et al.* 1967-1968
Euselasia euboea	(Hewitson, [1853])	Myrtaceae	*Eugenia pitanga* (O. Berg) Kiaersk.	Brazil	Silva *et al.* 1967-1968
Euselasia euboea	(Hewitson, [1853])	Myrtaceae	*Myrciaria chartacea* O. Berg	Brazil	Silva *et al.* 1967-1968
Euselasia euboea	(Hewitson, [1853])	Myrtaceae	*Myrciaria chartacea* O. Berg	Brazil	Monte 1934
Euselasia euboea	(Hewitson, [1853])	Myrtaceae	undetermined sp.	Brazil	Lima 1950
Euselasia eubule	(R. Felder, 1869)	Myrtaceae	*Eugenia costaricensis* O. Berg	Costa Rica	Janzen & Hallwachs 2009
Euselasia eubule	(R. Felder, 1869)	Myrtaceae	*Eugenia valerioi* Standl. [cited as *E. valerii*]	Costa Rica	Miller *et al.* 2006
Euselasia eubule	(R. Felder, 1869)	Myrtaceae	*Psidium guajava* L. [introduced]	Costa Rica	Janzen & Hallwachs 2009
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eucalyptus paniculata* Sm. [introduced]	Brazil	Brun *et al.* 1977
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eucalyptus paniculata* Sm. [introduced]	Brazil	Nagaraja 1983
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eucalyptus* sp. [introduced]	Brazil	Macedo 1976
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eucalyptus* sp. [introduced]	Brazil	Silva *et al.* 1967-1968
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eugenia pitanga* (O. Berg) Kiaersk.	Brazil	Silva *et al.* 1967-1968
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eugenia pitanga* (O. Berg) Kiaersk.	Brazil	Ronna 1934
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eugenia pitanga* (O. Berg) Kiaersk.	Brazil	Lima 1928
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eugenia uniflora* L.	Brazil	Silva *et al.* 1967-1968
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eugenia uniflora* L.	Uruguay	Biezanko *et al.* 1957
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eugenia uniflora* L.	Uruguay	Ruffinelli 1967

TABLE 1. (continued)

Butterfly species [note]	Author(s) and year	Host plant family	Host plant species and author [note]	Locality	Source
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Eugenia* sp.	Brazil	Lima 1928
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Psidium cattleianum* Sabine	Brazil	Beccaloni *et al.* 2008
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Psidium cattleianum* Sabine	Uruguay	Ruffinelli 1967
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	Psidium cattleianum Sabine	Uruguay	Biezanko *et al.* 1957
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Psidium guajava* L. [introduced]	Brazil	Lima 1947
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Psidium guajava* L. [introduced]	Brazil	Silva et al. 1967-1968
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Psidium cattleianum* Sabine	Brazil	Silva et al. 1967-1968
Euselasia eucerus	(Hewitson, 1872)	Myrtaceae	*Psidium* sp. [cited as Guayabenbaumes]	Brazil	Hoffmann 1931
Euselasia eugeon	(Hewitson, 1856)	Sapotaceae	*Chrysophyllum cuneifolium* (Rudge) A. DC. [cited as *C. cucumifolium*]	Paraguay-Argentina	Jörgensen 1932
Euselasia eugeon	(Hewitson, 1856)	Sapotaceae	*Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl.	Argentina	Hayward 1969
Euselasia eugeon	(Hewitson, 1856)	Sapotaceae	*Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl.	Paraguay	Jörgensen 1924
Euselasia eulione	(Hewitson, 1856)	Myrtaceae	*Psidium guajava* L. [introduced]	Ecuador	DeVries *et al.* 1994
Euselasia nr. *eulione*	----------	Myrtaceae	*Psidium* sp.	Ecuador	DeVries *et al.* 1994 / Beccaloni *et al.* 2008
Euselasia euryone	(Hewitson, 1856)	Clusiaceae	*Mahurea palustris* Aubl.	French Guiana	Brévignon 1997
Euselasia hieronymi	(Godman & Salvin, 1868)	Myrtaceae	*Eugenia capuli* (Schltdl. & Cham.) Hook. & Arn.	Mexico	Kendall 1976 / DeVries 1997
Euselasia hygenius	(Stoll, 1787)	Myrtaceae	*Eucalyptus grandis* W. Hill ex Maiden [introduced]	Brazil	Nagaraja 1983
Euselasia hygenius	(Stoll, 1787)	Myrtaceae	*Psidium cattleianum* Sabine	Brazil	Beccaloni *et al.* 2008
Euselasia hygenius	(Stoll, 1787)	Myrtaceae	*Psidium* sp.?	Brazil	Beccaloni *et al.* 2008
Euselasia hygenius	(Stoll, 1787)	Myrtaceae	*Eucalyptus urophylla* S. T. Blake [introduced]	Brazil	Zanuncio *et al.* 1990, 1995
Euselasia 'hygenius'DHJ01	(Stoll, 1787)	Clusiaceae	*Marila laxiflora* Rusby	Costa Rica	Janzen & Hallwachs 2009
Euselasia labdacus	(Stoll, 1780)	Clusiaceae	*Mammea americana* L.	Suriname	Sepp 1828-48, see also Möschler 1878
Euselasia labdacus	(Stoll, 1780)	Clusiaceae	*Mammea americana* L.	Suriname	Seitz 1924 (probably from Sepp 1828-48) / DeVries 1997
Euselasia melaphaea [cited as *E. apisaon*]	(Hübner, 1823)	Myrtaceae	*Eucalyptus* spp. [introduced]	Brazil	Zanuncio *et al.* 1990, 1995

TABLE 1. (continued)

Butterfly species [note]	Author(s) and year	Host plant family	Host plant species and author [note]	Locality	Source
Euselasia melaphaea	(Hübner, 1823)	Myrtaceae	*Eucalyptus* sp. [introduced]	Brazil	Anjos *et al.* 1986
Euselasia melaphaea	(Hübner, 1823)	Myrtaceae	*Eucalyptus cloeziana* F. Muell. [introduced]	Brazil	Zanuncio *et al.* 1990
Euselasia melaphaea	(Hübner, 1823)	Myrtaceae	*Eucalyptus paniculata* Sm. [introduced]	Brazil	Zanuncio *et al.* 1995
Euselasia melaphaea	(Hübner, 1823)	Myrtaceae	*Eugenia uniflora* L.	Uruguay	Biezanko *et al.* 1974
Euselasia melaphaea	(Hübner, 1823)	Myrtaceae	*Guajava cattleyana* (Sabine) Kuntze [cited as *Psidium cattleianum*]	Uruguay	Biezanko *et al.* 1974
Euselasia melaphaea [cited as *E. apisaon*]	(Hübner, 1823)	Myrtaceae	*Eugenia uniflora* L.	Brazil	Biezanko *et al.* 1978
Euselasia melaphaea [cited as *E. apisaon*]	(Hübner, 1823)	Myrtaceae	*Guajava cattleyana* (Sabine) Kuntze [cited as *Psidium cattleianum*]	Brazil	Biezanko *et al.* 1978
Euselasia midas	(Fabricius, 1775)	Clusiaceae	*Tovomita* sp.	French Guiana	Brévignon 1995
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Calyptranthes chytraculia* (L.) Sw.	Costa Rica	Janzen & Hallwachs 2009
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Eugenia acapulcensis* Steud.	Costa Rica	Janzen & Hallwachs 2009
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Eugenia costaricensis* O. Berg	Costa Rica	Janzen & Hallwachs 2009
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Eugenia hypargyrea* Standl.	Costa Rica	Janzen & Hallwachs 2009
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Eugenia salamensis* Donn. Sm.	Costa Rica	Janzen & Hallwachs 2009
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Eugenia monticola* (Sw.) DC.	Costa Rica	Beccaloni *et al.* 2008
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Psidium* sp.	Costa Rica	Harvey 1987b
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Psidium friedrichsthalianum* (O. Berg) Nied.	Costa Rica	Janzen & Hallwachs 2009
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Psidium guajava* L. [introduced]	Costa Rica	Janzen & Hallwachs 2009
Euselasia mystica	(Schaus, 1913)	Myrtaceae	*Psidium* spp.	Costa Rica	DeVries *et al.* 1994
Euselasia pellonia	Stichel, 1919	Vochysiaceae	*Vochysia guatemalensis* Donn. Sm.	Costa Rica	Janzen & Hallwachs 2009
Euselasia procula	(Godman & Salvin, 1885)	Melastomataceae	*Ossaea micrantha* (Sw.) Macfad. ex Cogn.	Costa Rica	Janzen & Hallwachs 2009
Euselasia procula	(Godman & Salvin, 1885)	Myrtaceae	*Eugenia* sp.	Costa Rica	DeVries 1997
Euselasia regipennis	(Butler & Druce, 1872)	Myrtaceae	*Eugenia truncata* O. Berg	Costa Rica	Janzen & Hallwachs 2009
Euselasia rhodogyne	(Godman, 1903)	Clusiaceae	*Clusia odorata* Seem.	Panama	DeVries *et al.* 1994
Euselasia rhodogyne	(Godman, 1903)	Clusiaceae	*Clusia quadrangula* Bartlett	Costa Rica	Janzen & Hallwachs 2009
Euselasia thusnelda	Möschler, 1883	Clusiaceae	*Caraipa* sp.	French Guiana	Brévignon 1997

*K. Nishida, in preparation. Note: The host plant, *Marila* sp. (Clusiaceae) for *E. chrysippe* listed in Beccaloni *et al.* 2008, is an error (D. H. Janzen, pers. comm. 2004).

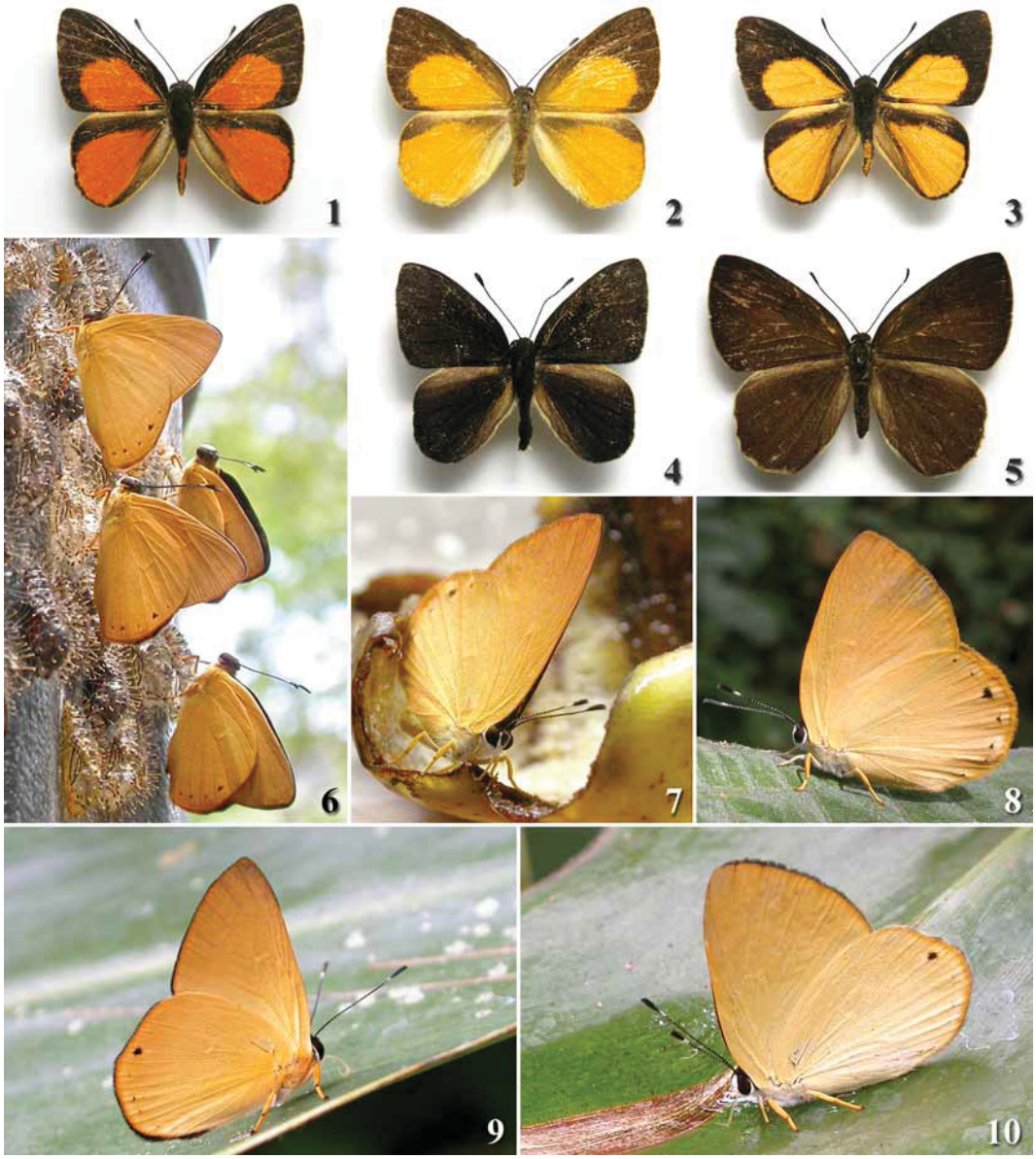
TABLE 2. Summary of parasitoid records for *Euselasia*. Voucher numbers, etc. from rearing data of Janzen & Hallwachs (2009) and other sources as indicated. Temporary voucher names in [ ]; Koino = koinobiont, Endo = endo parasitoid.

Host *Euselasia species*: Parasitoid names	Voucher code / source	Parasitoid family	Biological information
Euselasia bettina:			
Encarsia cf. *porteri* (Mercet)	this study	Ahelinidae	egg parasitoid
Telenomus sp.	this study	Scelionidae	egg parasitoid
Euselasia cheles:			
Calolydella [Wood01DHJ10]	07-SRNP-42208	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host prepupa.
Euselasia chrysippe:			
Encarsia cf. *porteri* (Mercet)	this study	Ahelinidae	egg parasitoid
Calolydella [Janzen01]	series of 04-SRNP-55192, etc.	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host prepupa.
Campylochaeta [Janzen01DHJ05]	series of 04-SRNP-55451	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host prepupa.
tachijanzen01 Janzen41	04-SRNP-55476	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host prepupa.
Calolydella sp.	this study	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host prepupa.
Euselasia 'hygenius'DHJ01:			
Houghia [Wood03b]	series of 99-SRNP-5220	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Houghia [Wood03bDHJ04]	series of 99-SRNP-5215	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Houghia [Wood27]	series of 04-SRNP-2924	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Euselasia melaphaea:			
Trichogramma maxacalii Voegele and Pointel	Oliveira *et al.* 2000	Trichogrammatidae	egg parasitoid
Euselasia mystica:			
chalJanzen01 janzen01	seirs of 06-SRNP-56653	Chalcididae	koino-endo, solitary, possibly attacks late instar, pupates in host pupa.
see voucher	02-SRNP-4037.20	Chalcididae	koino-endo, solitary, possibly attacks late instar, pupates in host pupa.
see voucher	04-SRNP-41146	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Podogaster guissellea Gauld [DHJ01]	series of 03-SRNP-3527	Ichneumonidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Podogaster guissellea Gauld	06-SRNP-20118	Ichneumonidae	koino-endo, solitary, possibly attacks late instar, pupates in host pupa.
Houghia [Houghia Wood03bDHJ04]	02-SRNP-33526, etc.	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Houghia [Wood27]	04-SRNP-2924, etc.	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Hyphantrophaga blanda (Osten Sacken) [DHJ06]	04-SRNP-48758, etc.	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Leptostylum [Janzen42]	series of 05-SRNP-49495	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.
Zizyphomyia [Wood06]	series of 06-SRNP-40252, etc.	Tachinidae	koino-endo, solitary, possibly attacks late instar, larva come out from host pupa.

Results

Life history of *Euselasia chrysippe*
(Figs. 1–50)

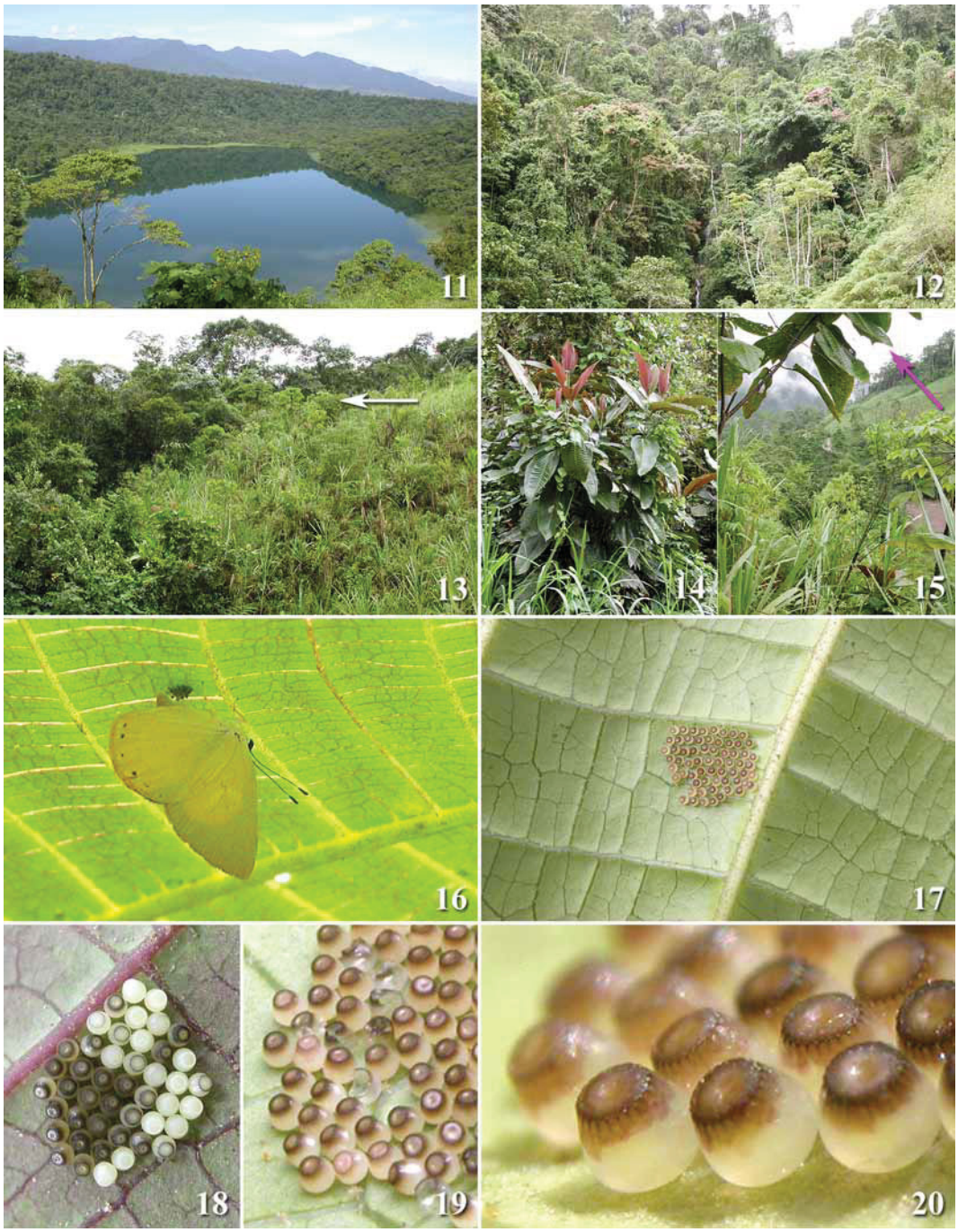
The life history of *Euselasia chrysippe* is similar to that of *E. bettina*.



FIGURES 1–10. Adults of *E. chrysippe* and *E. bettina*. **1)** Male *E. chrysippe* upper surface, Turrialba, reared; **2)** Female *E. chrysippe* upper surface; **3)** Male *E. chrysippe* in pale orange color form, upper surface, Turrialba, reared; **4)** Male *E. bettina* upper surface, Laguna de Hule, reared; **5)** Female *E. bettina* upper surface; **6)** Recently eclosed male *E. chrysippe*, Lake Arenal; **7)** Male *E. chrysippe* feeding on rotten banana peel under captive conditions in acrylic chamber, Lake Arenal; **8)** Female *E. chrysippe* resting on *M. calvescens* leaf, Lake Arenal; **9)** Male *E. bettina*, Laguna de Hule; **10)** Female *E. bettina* feeding on rain water on a leaf.

Habitat. All life stages usually were found in primary to secondary wet forests in light gaps, along trails, streams, rivers, gorges, valleys, and lakes. This includes the habitat surrounding Laguna de Hule (Fig. 11) (eggs and larvae found in December 2003), El Ángel-Cariblanco (eggs and larvae found in September 2002, December 2003), OTS La Selva Station (adults, eggs, and larvae found in January 2007, June 2008), the north

side of Lake Arenal (eggs, larvae, pupae found in August–November 2003), Hitoy Cerere Biological Preserve (larvae found in April 2004), and Jicotea, Turrialba (Figs. 12–15) (eggs, larvae, and pupae found in October 2000, September 2001, January, August, October–December 2002). Except for the adults (a few individual males resting on the underside of leaves of *Miconia impetiolaris* (Sw.) D. Don.) observed at La Selva Station, no adults were observed in the field.

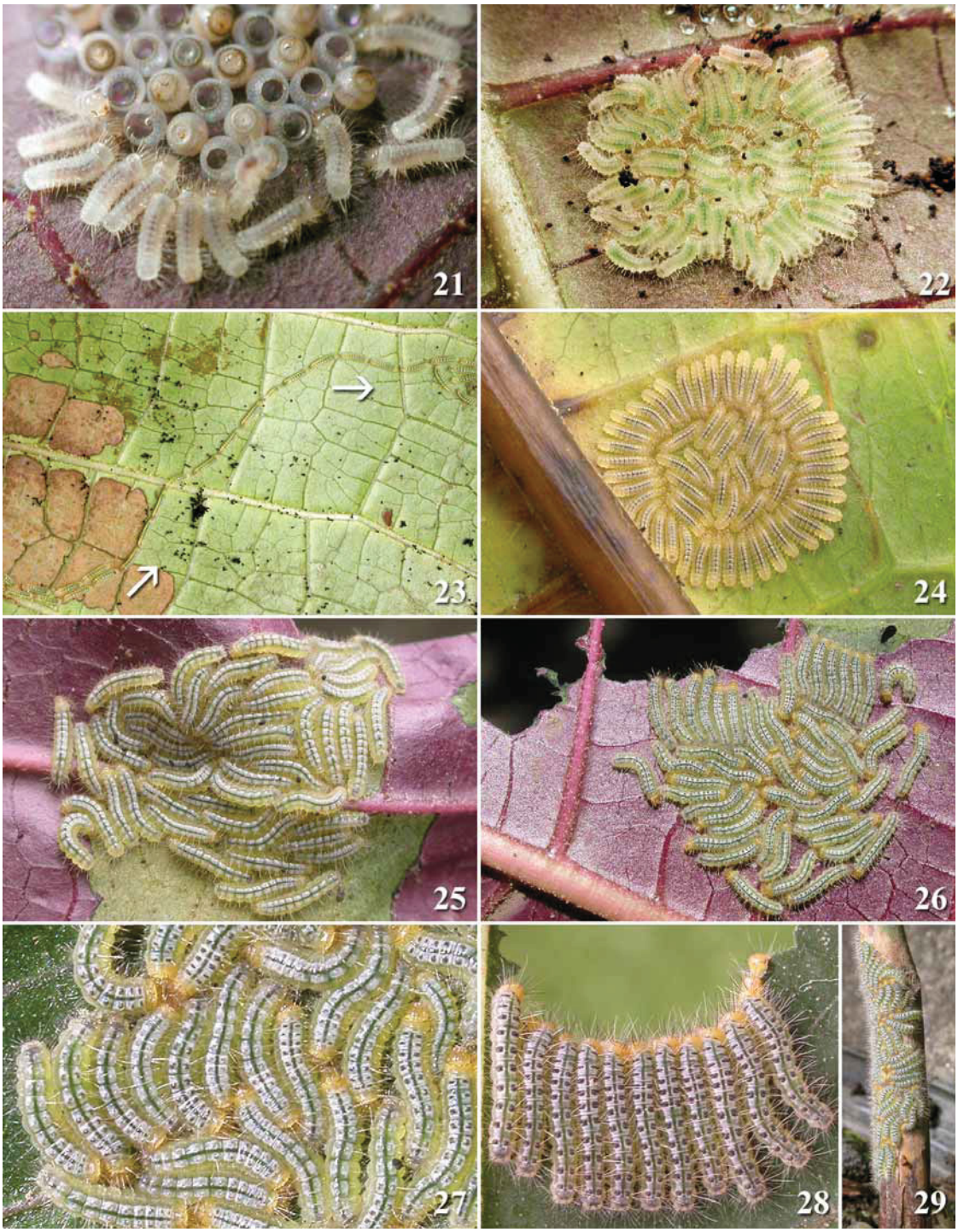


FIGURES 11–20. Life history of *E. chrysippe* and *E. bettina*, in part. **11)** Habitat of *E. chrysippe* and *E. bettina*, and *M. calvescens* at Laguna de Hule, Alajuela province, Costa Rica; **12)** Habitat of *E. chrysippe* and *M. calvescens* at a gorge in Jicotea-Turrialba, Alajuela province; **13)** Young trees *M. calvescens* growing on a steep hill among sugarcane at Jicotea site, arrow indicates young tree with larvae; **14)** Young trees of *M. calvescens*, approximately 2.5 m high, Jicotea; **15)** Close view of the young tree in figure 13, arrow indicates position of resting larvae; **16)** Female ovipositing at the Ecological Preserve, UCR; **17)** Egg mass, general dorsal view; **18)** White colored eggs; **19)** Unknown damage frequently found on clusters of eggs, dorso-lateral view; **20)** Close-up dorso-lateral view of eggs (note eggs raised from leaf surface).

Oviposition and eggs. Oviposition by some released females was observed in an open area on the west side of the river slope of the Leonelo Oviedo Preserve during September, 2003. Oviposition began about a week after eclosion and the release of laboratory-reared adults and lasted for approximately a week; Allen (2007) reported up to nearly four weeks. Females flew near planted *Miconia calvescens*, usually within 50 cm of the plant. The flight was fluttery, followed by perching on the underside of a leaf. The female before commencing oviposition rubbed her abdominal tip side to side against the leaf surface (n = 1). This female laid 45 eggs (Figs. 16, 18) in 30 minutes from the time of rubbing her abdomen until she left the oviposition site. Several bouts of oviposition were observed between 1100 and 1500 hours under conditions that varied from sunny to drizzly with an air temperature of approximately 26 °C.

Eggs (Figs. 16–21; 52–56 *E. bettina*) were laid in tight clusters, usually between primary veins on the underside of mature leaves. Each egg was elevated (Figs. 20 and 53; *E. bettina*) from the plant surface by a short stalk (Fig. 54; *E. bettina*). No overlapping of eggs (one on top of another), as noted by DeVries (1997), was observed during this study (n = 50 egg masses). The mean number of eggs in each cluster was 70 (SD = 20; range = 44–113; n = 29). At least some of the eggs in more than 33% of the egg masses collected at Lake Arenal (n = 30) were damaged, with conspicuous scattered remains of egg shells or displaced eggs (Fig. 19) and a few masses with dead eggs covered by fungal growth. Usually only one cluster of eggs was observed per leaf, although in some cases up to three clusters were present. Eggs were found mostly on leaves located ca. 30 cm from the tip of a branch on large (7.0–8.0-m tall) trees. In a few cases at Lake Arenal, eggs were found in the mid-portion of ca. 1.5-m tall saplings. At UCR Preserve where there were no large trees, several ovipositions were observed on 50-cm tall saplings. On large trees (n = 3 trees) at Lake Arenal (25–27 July 2003), approximately 30% of the mature leaves contained either eggs or larvae. No noticeable color change occurred in eggs prior to larval hatching.

Larvae and feeding. All of the laboratory-reared larvae molted five times, i.e., there are six-instars (n = 30 groups). Larvae were gregarious and processionary throughout their development. They were synchronous in their feeding, movements between sites, resting, and molting, as described by DeVries (1997). The first instar larvae (Figs. 21–24, 57–59) hatched 'synchronously' with each larva chewing out a circular hole along the egg rim (Fig. 21). During the first few hours after hatching, the group remained motionless around the egg mass (Fig. 21). After the entire group hatched, the larvae began to feed on the egg shells along the periphery of the egg mass. Most egg shells in the central part of the egg mass, except for the central stalked portion of each empty egg, were not fed upon (Figs. 22, 57). Larvae later formed a tight group and moved away, forming several lines (Fig. 57); they then formed a single line composed of the entire group. On the underside of the leaf on which eggs were laid, the larvae lined up side by side in a more or less circular pattern (Fig. 22) and fed on the lower epidermis and mesoderm of the plant, leaving the upper epidermis intact. Kendall (1976) described a similar behavior in *Euselasia hieronymi* (Godman & Salvin, 1868). This feeding resulted in damage ca. 7 x 20 mm to 20 x 40 mm of pale-brown to brown scar patches (Figs. 23, 60). After feeding, the larvae traveled in a single line, often in tail-to-head contact, to another feeding site on the same leaf (Fig. 23). Larvae usually fed continuously day and night until the pre-molting period. Otherwise, larvae were seldom observed resting between feeding; resting occurred in clusters on the underside of leaves (e.g., Fig. 33) and occasionally on leaf petioles or stems in mid- to late-instars (Figs. 29, 37, 69). Clumping behavior was described by Hoffmann (1931) in the larvae of *Euselasia eucerus* (Hewitson, 1872). Larvae molted on the underside of leaves, except in one case in which a group of fourth instars molted on a stem. The entire body color of the larvae became less translucent and pale yellowish-white in the pre-molting period in each early instar (Figs. 24, 59, 63). During mid- to late-instars, the pale color was more conspicuous on the head, thoracic segments, and last few abdominal segments. Before molting, larvae clustered in a tight circle with heads pointed inwards, usually between the primary central vein and primary side veins (Fig. 24). The larvae molted 'synchronously' within a short period of time to the second instar, and within a few hours moved in procession to a different feeding site on the same leaf. They did not feed on their molted skins and head capsules which sometimes remained attached to the leaf (also documented by Brévignon (1997) in *Euselasia euryone*) before moving to a new feeding site.



FIGURES 21–29. Life history of *E. chrysippe*. **21)** First instar hatching and lining up around the egg mass, dorsal view; **22)** First instar in rasp-feeding formation, dorsal view (note remaining of egg shells on top); **23)** Late stage first instar in procession, dorsal view, arrows showing direction of movement (note feeding damage on left); **24)** Pale-colored pre-molting stage first instar, dorsal view; **25)** Late stage second instar and its feeding damage, dorsal view; **26)** Mid-stage third instar and its feeding damage, dorsal view; **27)** Close-up of third instar, dorsal view; **28)** Mid-stage fourth instar feeding in parallel position on upper- and underside of leaf, dorsal view; **29)** Fourth instar larvae clustered and resting on host trunk near base.

Second instar larvae (Figs. 25, 61) continued to feed in the same manner as first instars. During the second instar prior to molting or the third instar after molting, the larvae (Figs. 26–27, 62–63) moved to another leaf.

Some groups of early third instar larvae fed on the leaf either by grazing the inferior surface, skeletonizing, or on the entire leaf tissue including thin veins (Fig. 26) (Feeding mode and mandibular morphology are detailed in the discussion.) Usually from the third instar onward (Figs. 26–37, 42–44, 62–73) the larvae chewed through the entire thickness of the leaf except for the primary veins. The remnants of primary veins were chewed off by the larvae in pieces of 10–15 mm long and dropped to the ground. The larvae usually lined up parallel to each other on the underside of a leaf apex as they fed on the entire thickness of the leaf (Fig. 39) and on occasion on both the upper and underside of the leaf (Figs. 28, 68, 72). Late instar larvae also fed on leaf petioles when the food source was limited. None of the 30 groups reared on potted plants fed on the purplish young leaves of the apical shoot (Fig. 41). Most of the feeding was on the peripheral areas of leaves and less on the area of the central primary vein. Thus, feeding damage left a more or less triangular central portion of the leaf intact (Fig. 39). This type of damage was also observed in the field.

Processionary behavior. After feeding, mature last instar larvae in captivity traveled in procession, searching for places to pupate (Figs. 43–44, 74). The procession lasted for a few hours (n = 2 groups), mostly along the rim of the flower pot in a circle (Fig. 74). Eventually, the procession broke, and the larvae split into several groups and clustered loosely, reaching the outer side of the flower pot. Each larva spun a loose platform of silk on the pot substrate and prepupated (Figs. 45, 75). Pupation occurred in clusters of a few to as many as 60 individuals (these 60 pupae occupied an area of ca. 11 x 6.0 cm flat surface), but some pupated singly (Figs. 46–47, 76–77). During field work, only three single pupae and one cluster of two pupae were found on undersides of host leaves. Despite careful searches of host tree trunks, tree bark of other trees in the vicinity, broad leaves of small plants, etc., no other pupae were observed in the field. Thus the 'usual' pupation site is unknown.

Processionary behavior (Figs. 23, 43–44, 57) was observed in all larval instars, from recently hatched first instar larvae (Fig. 57) to pre-prepupal stage larvae (Figs. 43–44, 74). The minimum number of larvae in a procession was two; a single larvae traveling along an apparent 'chemical trail' left by other larvae was also observed. When in a procession, the larvae were usually in tail-to-head contact in a directed single line, i.e., the posterior end of the larva in front frequently was in contact with the head of the larva behind. While marching, the contact was accomplished mostly by the long setae projecting posteriorly from the anal plate of the larva in front with the long setae projected forwards from the prothoracic shield of the larva behind (Figs. 43–44). However, it was not uncommon to see a break in the contact between adjacent larvae, with the space between two larvae frequently exceeding the total length of the setae. Even with the loss of tactile contact, larvae maintained the procession. Each larva also swung its head from side to side and laid silk on the marching substrate (Figs. 40, 43). When the procession halted, the head of each larva was pressed against the last abdominal segment of the larva in front of it (Fig. 43). Even in this situation the larva continued to swing the head from side to side. When viewed closely from the side, marching larvae were observed to drag the A10 prolegs and the lower tip of the last abdominal segment on the substrate.

One group of last instar larvae was observed ventrally through a plastic bag revealing that each time the larvae moved forward, they retracted their A10 prolegs and convexly expanded the middle part of the cuticle where claw-shaped setae (Figs. 206–207) are located. On the center of the convexly expanded cuticle, a semi-translucent concave 'spot' was present. In contrast, when not marching, the cuticle between the prolegs was retracted and concave; thus the claw-shaped setae were not in contact with the substrate. Additionally, several larvae in procession were observed drinking water droplets that adhered to the surface of the plastic bag.

During observations of behavior, I slightly manipulated the procession. When the 'leading' larva in the procession was removed, the following larva then led the procession (n = 4 removals). Each larva, including the 'leading' larva, stopped marching when it lost its setal contact with the larva behind (n = 10 stops). When the contact was reestablished, the larva in front began to march again (n = 10 reestablishment). When one of these halted larvae was pushed gently by a soft brush from behind (n = 4 pushes), the larva started marching. Marching larvae which were not in setal contact with each other 'preferred' following a more recently made, less-silkened trail instead of a slightly older trail which was heavily covered with silk (n >50 larvae, 3 groups).

FIGURES 30–41. Life history of *E. chrysippe*. **30)** Pre-molt third instar (arrows) intermixed with mid-fourth instar, dorsal view; **31)** Brown head mature fifth instar, dorsal view; **32)** Bright orange head mature fifth instar, dorsal view; **33)** Mid-stage sixth instar larvae on underside of leaf, dorsal view; **34)** Heads and caudal area of mid-stage sixth instar, fronto-lateral view (note head color variations); **35)** Head of sixth instar, frontal view; **36)** metallic-blue iridescence of sixth instar, lateral view of left A3–6; **37)** Mid-stage sixth instar clustered on stem and petiole area of potted host; **38)** Remains of dead sixth instar parasitized by *Calolydella* tachinid fly larva; **39)** Sixth instar feeding (note triangular form damage); **40)** Accumulated silk from procession of mature sixth instar on basal area of potted host; **41)** Feeding damage made by fifth and sixth instar on potted host (note remains of young leaves at apex).

FIGURES 42–47. Life history of *E. chrysippe*. **42)** A10, caudal view, showing general chaetotaxy and metallic-blue iridescence; **43)** Sixth instar tail-to-head contact, lateral view; **44)** Sixth instar larvae in procession, dorso-lateral view; **45)** Prepupae on side of flower pot surface; **46)** Pupae, dorsal view; **47)** Pupa, lateral view (note silken girdle on T3–A1).

Some larvae marching parallel in the same direction to another processionary line merged into one line. In order to merge, the line with the leading larva encountering another marching line usually waited on the side of the marching line. Then each larva on the waiting line either forcefully stuck its head in between two marching larvae or moved into the line when there was an available space between two larvae. When two oppositely marching lines encountered each other, i.e., lateral setae of larvae of each line were in contact, the larvae of the slower-moving line made a U-turn by breaking its line and merged into the faster-moving line, as described previously.

First instar larvae on host leaves traveled approximately 1.0 mm per second in a procession (n = 1 group, ca. 24°C air temperature); last instar larvae moved ca. 2.0 cm per second at their fastest pace (n = 1 group, ca. 30°C substrate surface temperature). In direct sunlight, the larvae on top of the leaf traveled rapidly to the underside where they made a large processionary mass with up to four parallel lines.

Auditory sensitive defensive behavior and other behaviors. Late instar larvae showed 'pulsed-head flicking' behavior only once against voice trials during the study (n = 30 groups and 30 voices total). This behavior (reacting to voice) was commonly observed in *Euselasia bettina*; these results are detailed in the section on *E. bettina*. The flicks appeared less vigorous and were repeated faster than those of *E. bettina*. The four groups of last instars feeding on leaves exposed to the sounds of violin pizzicato responded each time either with a single and rapid synchronized head retraction per exposure (and remaining motionless for a while) or less frequently, with 'weak' two to five head flicks after retracting the head. The motionless period diminished after each exposure to the sound. After about 10 exposures, the larvae simply responded to the sounds by retracting the head. Larvae in which SD2 setae on T1 shield had been removed responded significantly less to the sounds (2.43±1.27 SD) than the untreated larvae (9.30±1.10 SD) ($\chi^2_{\text{Yates}} = 22$, $P < 0.001$). In other words, larvae without setae usually continued to feed, showing no reaction to the sounds.

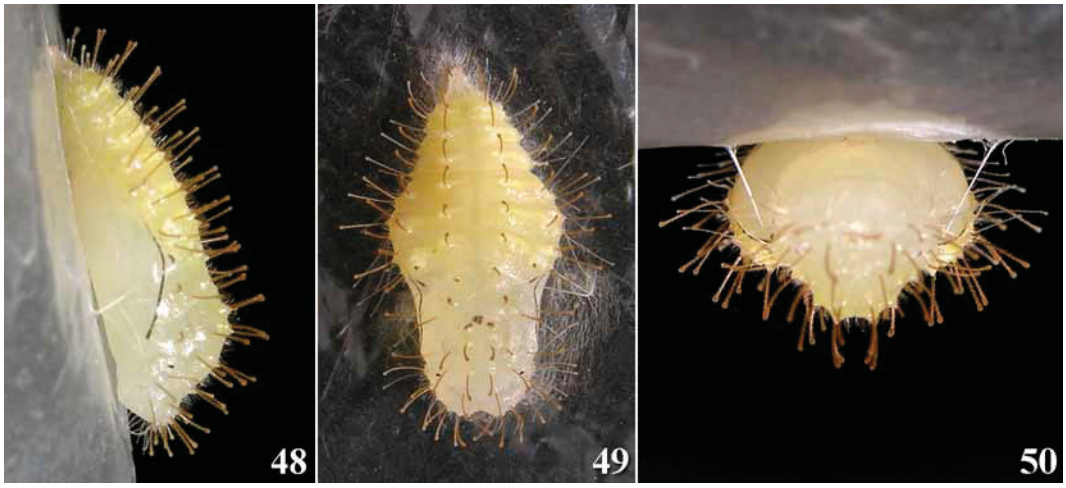
Late instar larvae frequently flicked the last abdominal segments either individually or simultaneously as a group while feeding, especially when they were disturbed, apparently by leaf vibration or contact from behind by other larvae that were wandering around. When pressed gently on the dorsal abdominal segments of fifth and sixth instars by a soft brush, the larva reacted by curling its body and/or with regurgitation of green fluid.

Intermixtures of different larval groups occurred both in the field and under laboratory conditions. When two or more groups of larvae in different stages and/or instars were placed on a single potted plant, they merged together as a single group and were reared successfully. For example, thirteen young fifth instars and 32 mature fourth instars that were preparing to molt were gathered into a single larval group (Fig. 30). In this condition, most of the young fifth instar larvae stayed still with the molting fourth instars without feeding. Furthermore, a group of *E. chrysippe* fifth instars and *E. bettina* sixth and fifth instars was feeding together on a leaf under rearing conditions (Fig. 68). In the field, a group of eleven mature second instars, 43 mature fourth, and one young fifth instar formed a group.

Pupation and pupae. Under lab conditions pupae usually were oriented vertically with their heads pointing downwards (n = 150) (Figs. 46–47; 76–77) although in a few the heads were oriented sideways. Most pupae on the flower pots were found on the shaded side (n = 142). Pupae were attached to the surface via a cremaster and densely-spun silk and secured by a silken girdle that passed over T3–A1 (Figs. 46–47; 76–77). The silk girdle was held by a silk-clipping structure (silk-clipper) on the dorsum of A1. When molested, the pupae jerked the anterior part of the body from side to side by laterally wiggling segments A5–10. Flexible intersegments were found between the A4 and 5, A5 and 6, and A6 and 7. When setae projecting laterally came into contact with the setae of another pupa, a chain reaction was triggered, and the entire group of pupae reacted similarly and continued to jerk for more than five minutes (n = 1 cluster of 9 pupae). When the setae were not in contact, the movement of a pupa did not trigger other pupae to start jerking. No audible sounds (e.g., creaking or clicking by 'stridulation') were noticed while the pupae reacted.

General coloration of the pupae varied between pale yellowish-white (Figs. 48–50) to brown with black (Figs. 46–47; 76–77). Differences in color appeared to be affected by the brightness (light intensity) of the surrounding microenvironment during the early part of the prepupal stage (see result of the experiment below). Under natural day-light conditions, pupae found on black flower pots in shaded areas were always darker than those in less shaded areas (n = ca. 300; 6 groups); larvae in transparent plastic bags, which pupated on the plastic bag in the shaded area (dorsally covered with leaves) were darker than those placed in areas without shade (n = 48; 2 groups). Larvae that pupated on host leaves also varied from pale-brown to brown with black according to the light intensity of the microenvironment (n = 23; 2 groups). Pupae on the plastic bag surface without shade were the palest (Figs. 48–50) (n = 13 pupae; 2 groups). About 24 hours prior to adult eclosion the eyes turned reddish-brown and the wings turned orange with black margins. About 12 hours prior to adult eclosion the entire body of the pupae became darker (Fig. 6).

All of the 32 prepupae on transparent plastic bags treated in dark environment in two different conditions turned brown with black pupae, i.e., there were no differences in coloration between the two treatments. This observation suggests that determination of color probably occurs in the early part of the prepupal stage, i.e., probably within a few hours after they fix themselves on the substrate.



FIGURES 48–50. Pale form *E. chrysippe* pupa. **48)** Lateral view; **49)** Dorsal view; **50)** Frontal view.

Adult eclosion. Adult eclosion (n = 7 groups) (Fig. 6) occurred somewhat synchronously (eclosed within less than an hour) but differed between the sexes. It occurred during the morning usually between 0800 and 1000 hrs with females eclosing approximately 24 hours prior to males. The ratios of emerging males to females reared from eggs were: 15:13, 15:29, 15:33, 40:66, the total being 85:141 (1:1.7) ($\chi^2_{\text{Yates}} = 13$, $P < 0.001$). The adults initiated weak short flights from approximately 1 hour after eclosion and longer flights 2–3 hours after eclosion. At night, adults rested on the side of the incubation chamber, with their heads oriented downwards. There were no observations of adults moving their hind wings back and forth against each other while at rest as suggested by Robbins (1985).

Eggs in females. Dissections of laboratory-reared females revealed that the numbers of eggs in the abdomen are as follows. In a female that was a few hours-old there were approximately 20 undeveloped (small and white) eggs and no developed eggs. When food was provided after eclosion, 25–30 more-or-less developed eggs (i.e., normal frustum shape, but not pigmented around the rim area) were observed in a 2–3 day-old female. Approximately 160 developed eggs and fifteen undeveloped eggs were found in the abdomen of three 10–15 day-old females. All these females were unmated.

Territorial, courtship, and mating behaviors. Territorial, courtship, and mating behaviors were observed under sunny conditions in the early morning between 0630 and 0730 hrs at the butterfly garden at Lake Arenal. In an open area of the sunny side of the garden, where a 2.5 m tall *M. calvescens* and several other plants with broad leaves were planted, four male *E. chrysippe* chased rapidly after a female at around 0640 hr. The flights occurred between 2.0–3.0 m above the ground. Other males were perched singly on top of broad leaves >2.0 m above the ground dashing out and chasing away 'intruders' (conspecific males or any other butterfly) that flew nearby. One pair was first seen in chase: the female landed on top of a leaf, and then the male landed right behind her. The male immediately opened and closed his wings 4–5 times per second and touched the caudal part of the female. Several seconds later the female flew away, and the male remained on the leaf. Between 0700 and 0710 hrs two mating couples were observed on the underside of leaves (10 x 4.0 cm in size) located in the south corner of the open area, approximately 2.5 m above the ground. After 0715 hrs, no *E. chrysippe* males chased females, although males perching on tops of leaves persisted. At 0740 hrs, the two mating couples were gone, so copulation probably lasted less than 30 minutes. Under captive conditions in the acrylic chamber, males and females that fed on the given food survived for more than three weeks. However, no courtship, mating, or oviposition occurred in the chamber.

Duration of each life stage. The average duration of each life stage reared under lab conditions follows (n = 12 groups). The egg stage lasted up to 28 days from the moment of oviposition. First instar lasted 4 days,

second instar 5 days, third instar 4 days, fourth instar 4 days, fifth instar 4 days, sixth instar 5–6 days (for a total of 26–27 days, with each instar having a pre-molting period of 1–2 days), prepupae 1 day, pupa 7 days for females and 8 days for males. Total duration from egg to adult eclosion was approximately 8 weeks. Observations of both male and female adults released in Reserva Ecológica Leonelo Oviedo suggest that adults live longer than a month (also see Allen 2007).

Parasitoids. Egg and larval parasitoids were reared during this study. A species of Aphelinidae, probably *Encarsia porteri* (Mercet) (all males, n = 280), was reared from eggs collected at Lake Arenal and El Ángel-Cariblanco. Parasitized eggs had a bluish-gray tint (Figs. 55–56) and then turned black. Adult aphelinids emerged from the upper surface of the eggs by chewing out a circular hole, ca. four-fifths of the top of the egg. The edge of the exit hole was ridged less regularly than holes made by *E. chrysippe* larvae. The rate of parasitism of egg masses collected was relatively low, approximately 18% of more than 50 egg masses collected; conversely, the rate of parasitism within each parasitized egg mass was high, reaching between 92 and 100% of eggs (n = 9).

A species of *Calolydella* (Tachinidae) was reared from each individual in a group of five recently molted last instar larvae collected at Jicotea, Turrialba (Figs. 13, 15). Prior to emergence of the *Calolydella* larvae, the *E. chrysippe* larvae dispersed along the host plant and remained motionless for approximately a day. After emergence of the *Calolydella* larva, the empty skin of the *E. chrysippe* larva was brownish and deflated and remained attached to the plant surface (Fig. 38).

Other host plants. Other host plants recorded for *Euselasia chrysippe* are *Miconia donaeana* Naudin (Melastomataceae) from Vereh, Turrialba, Cartago (E. Chacón, pers. comm. 2005) and *M. impetiolaris* (Sw.) D. Don. (pers. obs. 2007), *M. appendiculata* Triana and *M. longifolia* (Aubl.) DC. (E. Chacón, pers. comm. 2007) from OTS La Selva station near Puerto Viejo de Sarapiquí, Heredia. Additionally, leaves of *Clusia flava* Jacq. (Clusiaceae), two *Eucalyptus* spp. (Myrtaceae), *Eugenia truncata* O. Berg (Myrtaceae), and *Psidium guajava* L. (Myrtaceae) were also given to fourth to last instar *E. chrysippe* (collected on *Miconia impetiolaris* at OTS La Selva Station) and the larvae failed to feed on the leaves (no choice test, n = 2 groups); however, the larvae fed on leaves of *M. calvescens* on the UCR campus and completed the life cycle. These larvae also lined up parallel to each other and fed briefly (about 30 minutes) on the leaves of *Conostegia xalapensis* DC. These larvae continued to feed on *M. calvescens* and successfully completed the life cycle.

Life history of *Euselasia bettina*
(Figs. 11, 51–77)

In general, the life history of *E. bettina* is similar to of *E. chrysippe*. A few differences are detailed below.

The early stages were found at Laguna de Hule in September–December 2003 and at El Ángel-Cariblanco in December 2003. Adults were encountered more frequently in the field than *E. chrysippe*. *E. bettina* has been observed flying near the ranger station at Tapant National Park in Orosi (1250 m; 946'00"N, 8347'30"W) in late April and early July 2005 (pers. obs.), at Reserva Biológica Alberto Manuel Brenes (1013'12"N, 8436'6"W–1013'01"N, 8435'55"W; 850–1000 m) in San Ramón in late September 2004 (I. Nakamura, pers. comm. 2006) and mid-July 2005 (M. Hoshi, pers. comm. 2005), and in El Ángel-Cariblanco Region in July 2005 (E. Chacón, pers. comm. 2005).

Several groups of males chasing after females were seen mainly between 0730 and 0900 hrs in open areas along a road side under sunny conditions in all three sites mentioned above. Their flight was rather fast, and the animals flew in the same area between about 0.5 and 3.0 m above the ground. Males habitually perched on leaves in the same area where they were flying as mentioned by DeVries (1997).

The mean number of eggs (Figs. 52–56) in three clusters was 89 (SD = 9; range = 82–99). A recently eclosed female contained approximately 20 small undeveloped eggs and no developed eggs.

The pupation site is unknown under natural conditions. Male and female adults eclosed in the evening between 1800 and 2030 hrs under laboratory fluorescent light conditions in the acrylic chamber. It took approximately 30 minutes for newly eclosed adults to dry and expand their wings, and adults flew vigorously

within 90 minutes of eclosion in the chamber. The ratios of males to females emerging were: 18:12, 19:18, and 29: 27 ($\chi^2_{Yates} = 0.5$, $0.25 < P < 0.50$).

Some extraordinary larval behaviors include "enlarging the cluster and each larva freezing in an S shape" (S-shaped behavior) and "simultaneously and rapidly flicking their heads" (pulsed head-flicking behavior). The first behavior was not observed in *E. chrysippe*, whereas the latter was. The S-shaped behavior was observed only in mid- to late-stage second to fifth instar larvae of *E. bettina*. The larvae resting or molting on underside of leaves reacted to a leaf shake by moving themselves slightly away from the center of the tight cluster. Each larva moved backward and outward for a distance approximately equal to its body length. For example, large third instar larvae tightly clustered in a 23-mm diameter space expanded to approximately 45 mm. Each larva then became immobile, with its body in the form of a letter S, thus creating a mazelike pattern (Figs. 65–66). The larvae remained in this position for several minutes before slowly reforming the tight cluster.

The pulsed head-flicking behavior was observed in mid-stage fourth to mid-stage sixth instars. The larvae feeding in a parallel position responded to sounds, including the human voice (frequency probably between 230–310 Hz) and to other uncharacterized noises in the rearing environment. The larvae (n = 30) almost always responded by immediately discontinuing feeding, withdrawing their heads and remaining motionless for approximately a half second, then "simultaneously and rapidly flicking their heads" and thoracic segments dorsally about 15–20°, usually 3–5 times (in the absence of further sound emission). The larvae repeated the flicking when they were exposed to the sound again. The larvae also flicked their last three abdominal segments dorsally just after raising their heads. In the absence of further disturbance the larvae remained motionless and subsequently resumed feeding. The larvae reacted in the same manner when a piece of leaf vein was dragged gently onto the leaf surface and by moving or touching the leaf where larvae were feeding. They did not respond to the sound of weak hand-clapping and a higher pitched voice (ca. 580 Hz). When a mixture of fifth instar *E. chrysippe* and fifth and sixth instars of *E. bettina* larvae feeding together under captive conditions on a potted plant (Fig. 68) were exposed to the voice, only the *E. bettina* larvae responded with flicks (n = 5 voice trials). Applying a soft brush gently onto the dorsal abdominal setae of one of the feeding larvae for a split second caused only that larva to react with a single 'slow' flick of the head and thoracic segments, i.e., not pulsed as described above. The rest of the larvae did not react to this larval movement and continued to feed undisturbed.

A less frequently observed behavior was "drop down". While in procession, the mature last instar larvae occasionally dropped when they reached the tip of a leaf. The larvae behind followed and also dropped. This behavior resulted in drowning and high mortality of larvae under lab conditions. Larvae in procession behaved similarly when a finger was pressed softly against their abdominal segments. This behavior was not recorded in *E. chrysippe*.

Duration of each life stage follows. The eggs lasted up to six days (n = 2 groups, from moment of collecting). The first instar larva lasted six days (n = 2), second instar five days (n = 2), third five days (n = 2), fourth 4–5 days (n = 3), fifth four days (n = 3), sixth five days (n = 3). The entire larval stage lasted 30 days with each instar having a pre-molting stage of 1–2 days, prepupa one day, and pupa of females 8–9 days and males 9–10 days. Total duration from hatching first instar larva to adult eclosion was approximately six weeks in the lab (n = 2 groups).

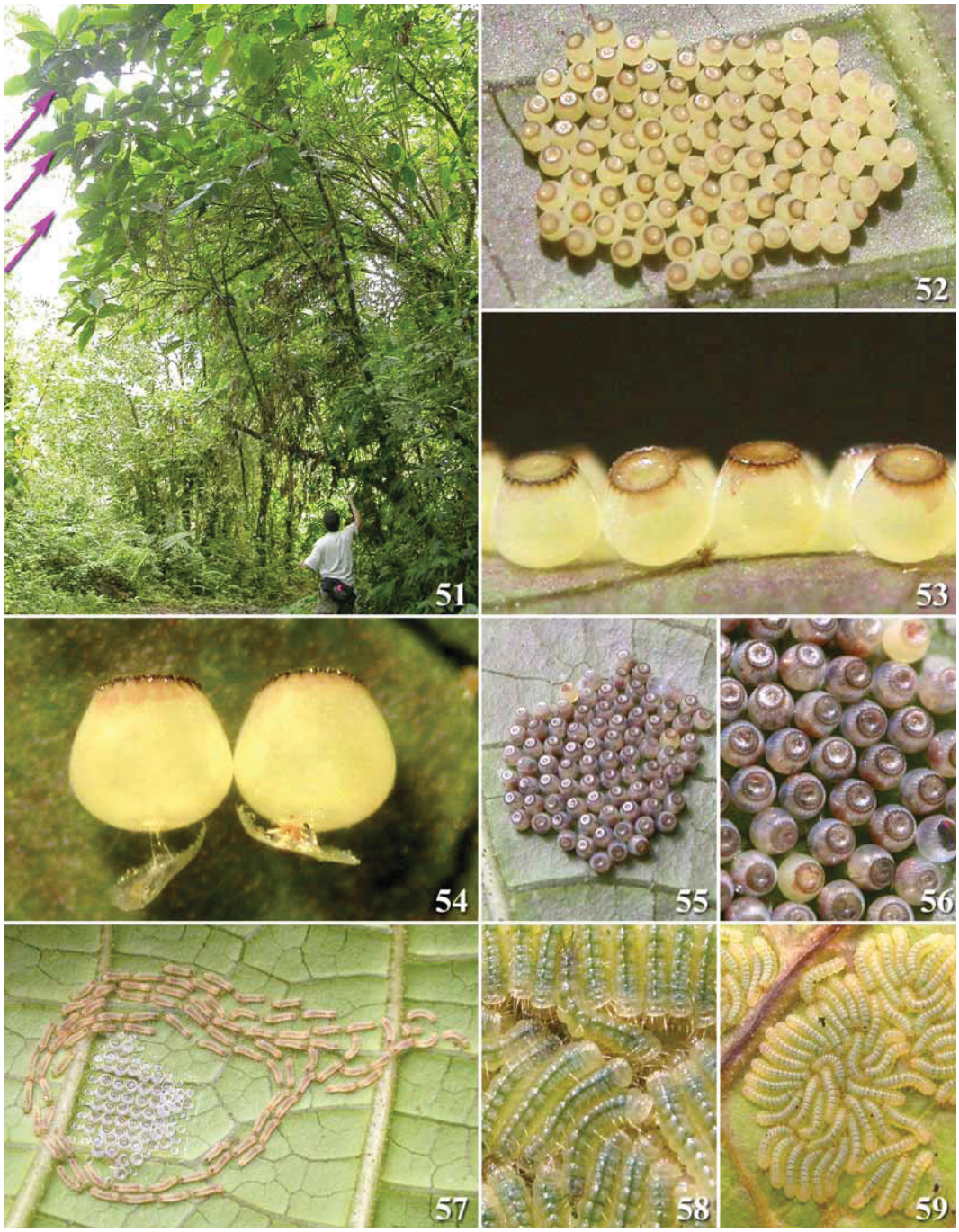
In addition to the same *Encarsia* parasitoid wasps of *Euselasia chrysippe* eggs, a *Telenomus* sp. (Scelionidae) was also reared from eggs collected at Laguna de Hule and El Ángel-Cariblanco. The parasitism rate of each egg mass was 75% and 96% (n = 2).

E. Chacón (pers. comm. 2006) recorded *Miconia theaezans* (Bonpl.) Cogn. from Reserva Biológica Alberto Manuel Brenes as another host plant of *Euselasia bettina*.

Third species of *Miconia*-feeding *Euselasia*

Several groups of eggs (Figs. 226–227) and larvae *Euselasia aurantia* (Butler & Druce, 1872) were found on *Miconia calvescens* and other *Miconia* species (Table 1) in the Central-Pacific Region along the Talamancan

range of Costa Rica (Burkhart 1995; Hawaii Department of Agriculture 1995; pers. obs. 2006). Adults of *E. aurantia* also have been collected at elevations between 100 m and 1700 m (INBio 1997–2006; Vega 2004; pers. obs.) from this region. In the early afternoon under very cloudy conditions along a river at Las Nubes de Santa Elena (0923'38.9"N, 8335'39.8"W; 1200 m), a female was observed ovipositing on *Miconia appendiculata* Triana.



FIGURES 51–59. Life history of *E. bettina*. **51)** *M. calvescens* (7.0–8.0 m tall) along trail at Laguna de Hule habitat. Arrows show area where a group of larvae was found; **52)** Cluster of eggs, dorsal view; **53)** Eggs, lateral view; **54)** Detached eggs showing stalk, lateral view; **55)** Cluster of eggs parasitized by a species of Aphelinidae, dorsal view; **56)** Close-up view of upper right area of figure 55 (note two un-parasitized eggs); **57)** Early stage first instar larvae forming procession, dorsal view, (note remains of egg shells; **58)** First instar feeding, close-up dorsal view; **59)** Pre-molting stage first instar, dorsal view.

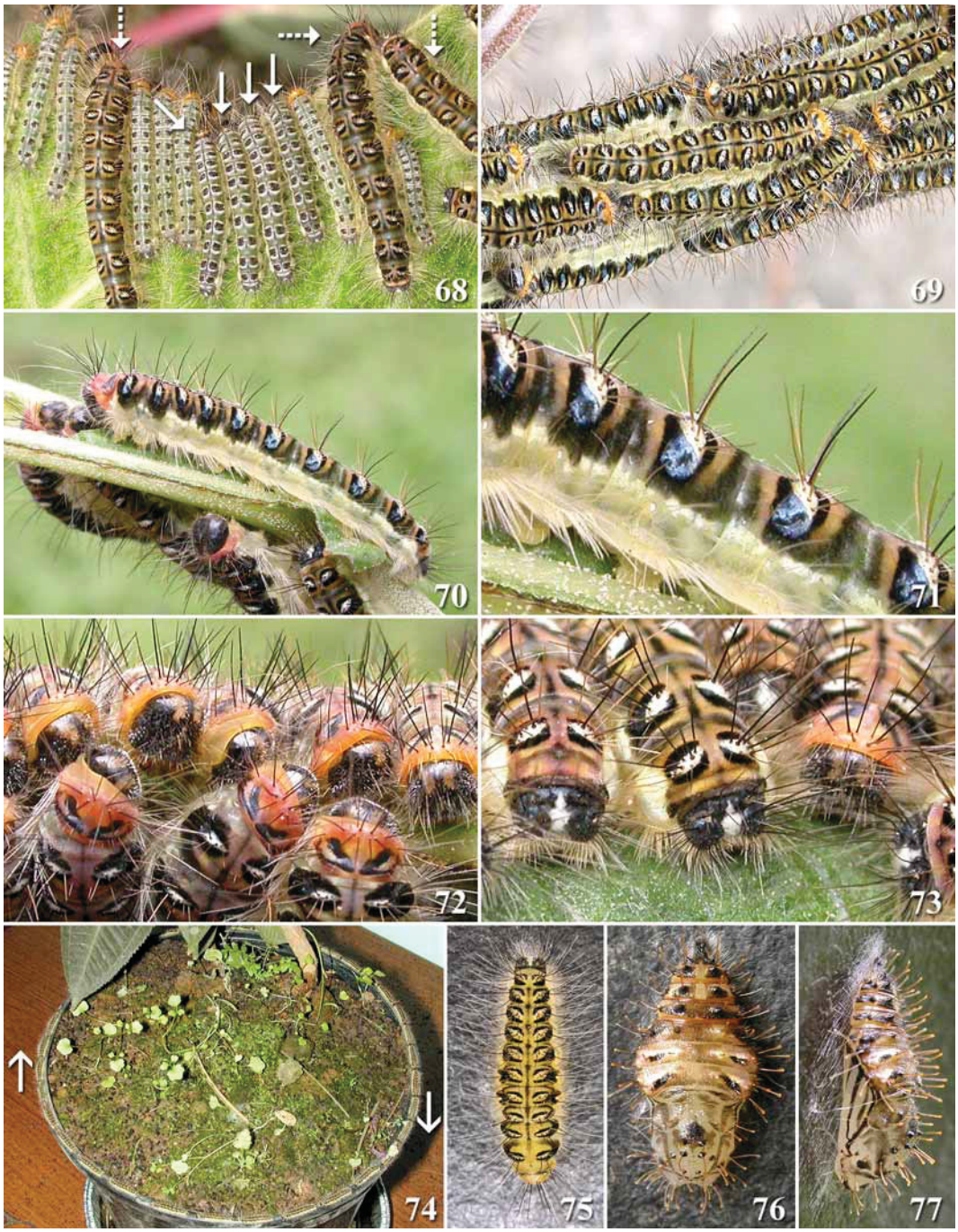
FIGURES 60–67. Life history of *E. bettina.* **60)** Old feeding damages made by early instars; **61)** Late stage second instar feeding, dorsal view; **62)** Mid-stage third instar resting, dorsal view; **63)** Pre-molting stage third instar and several recently molted fourth instar (darker individuals), arrows pointing at adhered molted larval skins; **64)** Late stage fourth instar, dorsal view; **65)** Late stage fourth instar showing S-shaped behavior, dorsal view; **66)** early stage fifth instar showing S-shaped behavior, dorsal view; **67)** Late stage fifth instar resting on young leaves, dorsal view.

Diagnosis and description of early stages of *Euselasia chrysippe*

EGG

Diagnosis: The egg of *Euselasia chrysippe* is semi-translucent pale-brown and ca. 0.42 mm in diameter. Pigmentation in the lateral wall extends beyond the apical rim up to ca. one-third of the egg height. The width of the crenulated rim area is ca. one-fifth of the dorsal surface diameter. The apical rim is purplish dark brown.

The rosette of the third row lacks closed cells. The egg of *E. bettina* is less translucent and yellowish pale brown (creamy-white), slightly larger (0.45 mm diameter), with narrower pigmentation, extending beyond the apical rim to ca. one-sixth of the egg height, and the width of the crenulated rim area is narrower, ca. one-seventh of dorsal surface diameter. The apical rim is purplish brown. The rosette of the third row has several closed cells.



FIGURES 68–77. Life history of *E. bettina.* **68)** Late stage sixth instar (dashed arrows) and mid-stage fifth instar (solid arrows) with mid-stage *E. chrysippe* fifth instar (no arrows) feeding; **69)** Mid- to late stage sixth instar resting on potted host stem, dorsal view; **70)** Mid- to late stage sixth instar feeding, lateral view; **71)** close-up of larva showing iridescence (A2–6) of figure70; **72)** Cephalic view of sixth instar feeding; **73)** Caudal view of sixth instar (cephalic view on upper right larva); **74)** Mature sixth instar showing processional behavior on rim of flower pot (arrows indicating direction of movement); **75)** Prepupa, dorsal view, head pointing downwards; **76)** Pupa, dorsal view; **77)** Pupa, lateral view (note silken girdle spun around T3–A1 and silken substrate).

Description: (Figs. 17–20, 78–89). Upright, frustum-shape, broadly rounded vetrnally (Figs. 20, 78–79, 84, 53–54), with basally attached stalk (Figs. 78–79, 87, 54), ca. 0.42 mm in diameter (widest at one-third from lower bottom), ca. 0.4 mm tall, generally semi-translucent pale-brown with apical rim area purplish-dark-brown; coloration may vary within a cluster from entirely white to dark purple near micropyle and/or apical rim and beyond (Figs. 18–19); chorion smooth up to ca. 64X magnification, but weakly sculptured (see below), semi-translucent to opaque; micropyle area (Figs. 80–81) slightly concave with a rosette sculpturing with 3–5 micropyles more or less evenly distributed along inner hub; rosette composed of three rows of very shallow ridged polygons. The first row consisting of 9–13 closed cells, second row with 14–19 (mostly) closed cells, third row without closed cells (n = 4); dorsal surface including and surrounding rosette with slightly raised repetitive concentric circles (Fig. 81); dorsal surface brown to purplish brown from micropyle, beyond a darkly pigmented, shallowly crenulated apical rim, up to ca. one-third of egg height on lateral wall, i.e., edge (height) of the lateral wall pigmentation uneven (Fig. 20); crenulate rim ca. one-fifth of dorsal surface diameter, porous, and outer portion confluent with vertically arranged and evenly distributed short lateral ridges (Fig. 80); lateral ridges with 2–3 crests, each crest with an apical aeropyle (Fig. 80); latero-ventral aspect broadly rounded (Figs. 20, 78–79, 84, 53–54); chorion with shallow hexagonally arranged wartlike structures, each structure connected with shallow ridges, more conspicuous near ventral aspect (Figs. 84, 87); venter slightly concave, with a raised domelike stalk connecting structure in the center (Figs. 82–84); stalk connecting structure ca. 80–100 μm wide (n = 5), irregularly ridged and porous (Fig. 83), with a wide basal stalk (Figs. 79, 87), absent on eggs extracted from female abdomen (probably a product of secretion from accessory gland); stalk translucent with brownish tint (Fig. 54), flexible, slightly elastic, ca. 0.09–0.12 mm long and 0.04 mm diameter in middle portion (narrowest), base width up to 0.25 mm (n=12); a thin, inconspicuous, membranous part of stalk extended beyond connecting structure up to ca. 100 μm radius, i.e., ca. one-fourth of egg width; wide stalk base with fiberlike extensions (Figs. 79, 87), fiberlike structure (probably originated from remnant of accessory gland fluid running through grooves on plant surface before hardening); center portion of inner surface of ventral chorion (opposite surface of stalk conjunctional structure) slightly raised and concave (Figs. 85–86); concave area with more or less hexagonally shaped grooves (Fig. 86).

Materials examined: Lake Arenal, 2003 (SEM, n = 4 complete specimens and 3 shells).

FIRST INSTAR LARVA

Diagnosis: The head capsule width of *Euselasia chrysippe* is ca. 0.20 mm; the head is translucent pale-brown; the body is semi-translucent white to pale-brown; and the prolegs on A10 have 7 crochets in a lateroseries. In *E. bettina* the head capsule is wider (ca. 0.25 mm); the head is slightly darker; the body is less translucent (creamy); and the prologs on A10 have 8–9 crochets in a lateroseries.

Description (Figs. 21–24, 90–135, 146–147): Body length 0.8–2.1 mm, initially semi-translucent white to pale-brown, with trace of brown internal organs (Fig. 21) which gradually change to pale-green upon commencement of feeding on plant tissue (Figs. 22–23), more white (less translucent) during pre-molting period (Fig. 24); integument covered with microtrichia, but less dense or absent on T1 shield, anal plate, and pinacula. **Head** (Figs. 92–97): Hypognathous, circular, slightly compressed laterally, ca. 0.20 mm wide, semi-translucent pale-brown; stemmata (Figs. 21, 93–96) dark-brown, 1–5 arranged in crescent and equally spaced, except 5 slightly distant from 4, 6 distantly positioned and equidistant from 1–5; oral area brown; setal groups A, C, F, L, P, SS, and S1–2 with setae nearly equal in length, long, ca. same length as epicranium suture, with micro-projections along mid-portion; MD-group microscopic; AF and S3 short, ca. one-fourth to one-fifth length of A, C, F, L, P, SS, and S1–2 setae, without micro-projections (Figs. 93–96); AF1 contiguous with mid-portion of adfrontal suture; AFa near dorsal angle of frons; AF2 lateral to dorsal angle of frons and dorso-laterally mesal to AFa; A1 at mid-distance between stemma 3 and C2; A2 laterally between AF1 and stemma 3; A3 between stemma 1 and P1; MD1–3 microscopic; MDa contiguously dorso-mesal to MD3; C1 and C2 above clypeus near lower angle of frons, C1 distal to adfrontal suture and C2 proximal to adfrontal suture; F1 near lower angle of frons dorsal to clypeus; Fa contiguously dorso-mesal to F1; L1 lateral to A3 and dorso-lateral to stemma 1; P1 lateral to intersection of epicranial suture and ecdysial line; P2 dorso-lateral and

slightly mesal to P1, more or less equidistant from MD1 and P1; S1 posterior to stemma 3; S2 dorso-posterior to stemma 6; S3 posterior to and slightly ventral to stemma 6; SS1 between antennal socket and galea; SS2 posterior to stemma 5; SS3 posterior to antennal socket in ventral aspect. Labrum (Fig. 97) with M1 near meson, shorter than M2; M2 between M1 and LA2; M3 ventral to M2, same length as M1; LA1 projecting from inner surface, dorsal to LA2 and shorter than LA2; LA2 lateral to M2 and as long as M2; LA3 ventral to LA2 and lateral to M3. Mandible (Fig. 146) with six large palmate teeth; inner surface weakly concave; mandibular setae subequal, longer seta with micro-projections near middle (Fig. 147); sensilla of antenna as figured (Fig. 98); maxillary palpus and sensilla as figured (Figs. 99–100). **Thorax:** T1 (Figs. 90, 92, 101–114): Shield (Figs. 90, 92, 101–104, 106) with six pairs of setae, XD1 (XD1a, b) and XD2 (XD2a, b), semi-translucent white to pale-brown, situated along anterior margin, more or less evenly distributed, projecting forward; XD1b slightly posterior to anterior margin; XD1b, D1–2, and XD2b thicker and longer than other setae; D1–2 dark-brown, projecting upward; all setae except SD2 with micro-projections along entire length; circular tablet organs (= flat cylindrical to circular tabletlike sensillum or lenticle) (Figs. 90, 101–105, Table 3) on anterior margin near middle, ca. 2.0 times as wide as but shorter than XD1a setal socket base, pores absent under 1530X magnification, flanked by XD1a and D1; cupola organ (= sensillum campaniformium, G.T. Baker, pers. comm. 2006) in form of slightly raised ring base with slightly raised papilla in center (Figs. 90, 102, 104, Table 3) posterior to XD1b, base ca. one-half of XD1b socket base, papilla one-third of base, perforations absent; D1 equidistant and diagonally behind circular tablet organs and cupola organ; D2 posterior to XD2a; pore (Da) between D1–2; two spherical organs (= sensillum in form of sphere on concave plate) (Figs. 90, 102–103, 106–107, Table 3) along latero-frontal margin, with shape varying from flat to papilloid, concave base plate ca. one-half of D2 setal socket, sphere one-half of base; subdorsal porton of shield along inner lateral margin slightly concave (= subdorsal groove) (Figs. 101–103, 106); SD1 absent; SD2 (= sensory seta, D.J. Harvey, pers. comm. 2006) (Figs. 90, 92, 101–103, 106, 108–109) featherlike, on anterior portion of subdorsal groove, projecting dorso-posteriorly, semi-translucent white to pale-brown, ca. three-fourths length of XD1 or D-group on shield, thinner than other setae on shield, narrower at base, loosely socketed in dome-shape pinaculum (Fig. 108); L1 semi-translucent white to pale-brown, on pinaculum in middle of segment, as long and spinose as XD1b, D1–2, and XD2b, but slightly thinner (Figs. 90, 92, 101–103, 110); L2–3 absent; spiracle circular (Figs. 90, 92, 103, 110); SV-group setae semi-translucent white to pale-brown, bisetose (Figs. 90, 92, 110); SV1 projecting laterally and SV2 slightly forward and downward; spherical organ diagonally below and posterior to SV1 on pinaculum (Figs. 9, 110); V1 short, simple (Figs. 90, 111); V2 absent; bladelike seta (Figs. 90, 92–97, 111–114, Table 3), nearly as long as coax plus femur, on pinaculum of basi-anterior portion of coxa, semi-translucent white, large and broadly flattened, ca. 3 times as long as wide, with longitudinal ridges, occasionally with a few dentations on apical part; leg setae with spatulate-tip, located mesally (Harvey 1987a, 1987b; somewhat similar to structure in microlepidoptera, e.g., Davis *et al.* 1992 and Davis 1999) (Figs. 93–94, 96, 111, 115, Tables 3–4), two spatulate-tipped setae on tarsus, as long as tarsal segment, projected downward from above claw, robust, dorso-ventrally flattened with stout longitudinal ridges dorsally reaching spatulate area, laterally widened, length of spatulate-tip approximately half-length of entire seta, 1.5 x as wide as basal area, spatulate-tip weakly curved upward (dorsally) and apex sharply to smoothly pointed, ventral surface more or less flattened and rough; absent on tibia and femur. T2–T3 (Figs. 90, 92, 101–103, 111, 115, 119): A pair of pinacula on dorsum, transversely narrow, with D-group setae; D1 dark brown, D2 semi-translucent white to pale-brown, nearly one-half length of D-group setae on T1, both with micro-projections, projecting upward (Figs. 90, 92, 101–103); SD1 (Figs. 90, 103, 119) in mid-lateral portion without pinaculum, short, simple; L-group (Figs. 90, 92, 95, 103, 111) trisetose, grouped together on pinaculum projecting laterally, L1 slightly backward, L2 slightly forward, and L3 slightly downward, semi-translucent white to pale-brown with micro-projections, slightly shorter than L1 on T1; spherical organ anteriorly between SD1 and L-group (Figs. 90, 95, 103); SV-group as in T1, but spherical organ absent (Figs. 90, 95, 111); two spatulate-tipped setae on tarsus, about as long as tarsus, two on tibia, similar to and about 2 times as long as spatulate-tipped setae on tarsus, but basal part of seta more cylindrical; spatulate-tipped setae absent on femur (Figs. 111, 115, Tables 3–4); bladelike seta and V1 as in T1 (Figs. 90, 111). **Abdomen:** A1 (Figs. 90, 92, 118–119, 122–123): Pinacula on dorsum wider than those on T2–3; D1–2 brown to pale-brown

with micro-projections, ca. 1.5 times longer than D-group setae on T2–3, bifurcate near base, ca. 0.15–0.17 total length of seta, thicker branch projecting outward, thinner branch projecting inward (Figs. 90, 92, 117–118, 120, Table 3; Samson *et al.* (1999)); spherical organ (Figs. 90, 118, Table 3) contiguous with inner-posterior portion of D1 on dorsal pinaculum, same size as in T1 shield; SD1 and subdorsal spherical organ near spiracle as in T2–3 (Figs. 90, 119, Table 3); spiracles as in T1; L-group with five setae projecting laterally, three in middle on same pinaculum, similar to those on T2–3 (Figs. 90, 92, 119); SV-group absent; flat seta (small bladelike seta) on subventral area (Figs. 90, 122–123, Table 3), ca. two-thirds length of bladelike seta on T1–3, anterior-caudally flattened, somewhat similar to bladelike seta but smaller, projecting ventrally; SV-group absent; V1 longer than those of T1–3, V2 absent (Figs. 90, 122–123). A2 (Figs. 90, 92, 116, 119, 122–123): As in A1 except color of D1–2 semi-translucent white to pale-brown, V-group bisetose, V2 mesally contiguous with flat seta (Figs. 90, 122–123). A3 (Figs. 90, 92, 122, 124): As in A1–2 except ventrally flat seta absent and proleg present (Fig. 124); SV-group with seven setae, SV1–4 grouped together laterally on pinaculum of proleg, SV5–7 on anterior part of proleg (Figs. 90, 92, 124); V-group trisetose (Figs. 90, 124); proleg with 5–6 uniordinal crochets in mesoseries, interrupted in middle, with a short 5–6 lateroseries, i.e., three separate rows of 5–6 crochets arranged in a subtriangular pattern on planta in center (Figs. 124–126). A4–6 (Figs. 90, 92, 125–126): As in A3 except spherical organ on inner-posterior of D1 absent, replaced by perforated plate organ (Figs. 90, 120–121, Table 3), larger than spherical organ, diameter similar to D1 socket base, concave and platelike with pores in center. A7 (Figs. 90, 92, 120–121): Same as in A4–6 except venter same as in A1, flat seta somewhat more slender than those of A1–2. A8–9 (Figs. 90, 92, 127–131): Similar to A7 but with segments apparently fused laterally (A8+9), separated dorsally to subdorsally and subventrally to ventrally (A8–9). Dorsal and subdorsal portion of A8 with organ (either spherical organ or perforated plate organ) absent on pinaculum posterior to D1; D1 bifurcate, D2 (not bifurcate) slightly longer than D1 (Figs. 90, 92, 128); SD-group absent; subdorsal spherical organ anterior to spiracle absent; spherical organ posterior to spiracle (= spiracle spherical organ) near A9 (Figs. 90, 128–129, Table 3). Dorsal and subdorsal portion of A9 with D- and SD-group absent; spherical organ posterior to spiracle spherical organ of A8 (Figs. 128–129, Table 3). Lateral portion of A8+9 (Figs. 90, 127) with L-group with eight setae, six in middle on pinacula (Figs. 90, 127). Subventral and ventral portion of A8–9 (Figs. 90, 130) as in A7, but V1 slightly shorter (Figs. 90, 130). A10 (Figs. 90–92, 127–135): Anal plate with eight pairs of long, slender and stout setae with micro-projections, a pair of short microscopic setae, and two pairs of cupola organs (Figs. 90–91 128–129, 132–133, Table 3); chaetotaxy as in Figs. 90–91, 132 and as follows: two pairs of long, stout setae similar to those on XD- and D-group on T1 shield, evenly distributed dorsally along anterior margin of plate; a pair of short microscopic setae similar to SD1 seta on T2–A7 slightly posterior between two stout setae of anterior margin; lateral edge with a pair of long, stout setae similar to XD- and D-group on T1 shield projecting posterio-laterally; middle portion of plate with two pairs of long, stout setae similar to XD- and D-group on T1 shield evenly distributed and projecting caudally; two pairs of less stout setae similar to L-group on A8+9 projecting caudally from between posterior of three pairs of setae in middle portion and lateral edges; a pair of slender setae similar to L-group on A8+9 projecting dorso-laterally from anterior to each lateral edge setae; cupola organ anterior to slender seta on lateral edge (Figs. 90, 128–129, Table 3), another cupola organ slightly posterior to setae in middle portion and anterior to inner pair of slender setae (Figs. 90–91, 132–133); SV-group with four short hairlike setae (Figs. 90, 130–131), spherical or papilla-shaped spherical organ above SV-group pinaculum (Figs. 90, 127, 130); "PP" (=paraproctal seta) on each side of posterior end of prolegs (Figs. 90, 130, 132); V1 located anterior to proleg (Figs. 90, 130, 134); eight claw-shaped setae (apparently paired) (Figs. 90, 130, 134–135, Table 3) between prolegs, stout, cylindrical, curved apically, 4 times as long as wide, shorter than V1 and SV setae; proleg with seven uniordinal crochets in lateroseries forming semicircle and with 4–5 uniordinal crochets in mesoseries arranged in a semicircle with a median gap.

Materials examined: Lake Arenal, 2003 (SEM, n = 3; dissecting stereo-microscope, n = 2).

Table 3. Summarized table of unique organs and setae in each larval instar of *Euselasia*. Numbers in parenthesis refer to numbers of characters presence on one side. ---------- = data unrecorded.

Characters	1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar
head: AHS	absent	present	present	present	present	present
body: AHS	absent	present	present	present	present	present
T1 shield: CTO on anterior-mesal	present (1)	absent	absent	absent	absent	absent
T1 shield: CTO on posterior-lateral	absent	present (2–3)	present (3)	present (9–10)	present (17–20)	present (30–40)
T1 shield: SO on anterior-lateral	present (2)	absent	present (1)	-	-	-
T1 shield: CO on anterior-middle	present (1)	present (1)	present (1)	-	-	-
T1 shield: D2	present	present	present	present	present	present
T1–3 legs: BLS	present	present (smaller)	present (smaller)	present (smaller)	present (smaller)	present (smaller)
T1–3 legs: STS	present	present	present	present	present	present
A1–8: bifurcated D group	yes	no	no	no	no	no
A1–2 and A7–9: FS on subventer	present	present	present	-	-	absent
A10: CS between prolegs	present (8)	present (8)	present (12)	-	-	present (ca. 40)
A10 shield: CTO in anterior-lateral	absent	present (3+1seta or 4)	present (4+1seta or 5)	present (5–7)	present (14–15)	present (33–36)
Organs on T1						
SO near spiracle	absent	absent	absent	-	-	-
spiracle PCO	absent	absent	absent	absent	absent	absent
SO on SV pinaculum	present (1)	present (1)	present (2)	-	-	present (10)
organ on mid-anterior portion of shield	absent	SO (1)	SO (1) or 1 seta	-	-	-
Organs on T2						
SO bt/ SD- and L-group	present (1)	present (1)	absent	-	-	present (5)
SO on SV pinaculum	absent	absent or present (2)	absent	-	-	present (3)
organ behind D1 seta (bt/ D1–2)	absent	absent	absent	-	-	SO (3)
organ on mid-anterior of pinaculum on dorsum	absent	SOl (1) or absent	SO (2) or AHS (1)	-	-	-
Organs on T3						
SO bt/ SD- and L-group	present (1)	present (1)	absent	-	-	present (5)
SO on SV pinaculum	absent	absent or present (1–2)	absent	-	-	present (3)
organ behind D1 seta (bt/ D1–2)	absent	absent	absent	-	-	SOl (10)
organ on mid-anterior of pinaculum on dorsum	absent	SOl (1)	SOl (1)	-	-	-
Organs on A1						
SO near spiracle bt/ SD- and L-group	present (1)	present (1)	present (4)	-	-	-
spiracle PCO	absent	absent	absent	-	-	-
organ behind D1 seta (bt/ D1–2)	SO (1) (papilla shaped)	SO (1)	SO (1)	-	-	SO (3)
Organs on A2						
SO near spiracle	present (1)	absent or present (1)	present (1)	-	-	-
spiracle PCO	absent	raised (1)	absent	-	-	-
organ behind D1 seta (bt/ D1–2)	SO (1) (papilla shaped)	SO (1)	SO (1)	-	-	-
Organs on A3						
SO near spiracle bt/ SD- and L-group	present (1)	absent or present (1)	present (2–3)	-	-	present (3–5)
spiracle PCO	absent	raised (1)	raised (1)	-	-	raised, flat, or sunken (24–33)
organ behind D1 seta (bt/ D1–2)	SO (1) (papilla shaped)	SOl (1)	SOl (1)	-	-	-
Organs on A4						
SO near spiracle bt/ SD- and L-group	present (1)	present (1)	present (1–3)	-	-	present (1)
spiracle PCO	absent	flat (1)	flat, raised, or sunken (4)	-	-	raised or sunken (25–17)
organ behind D1 seta (bt/ D1–2)	PPO (1)	SOl (1)	SO (1)	-	-	-

.....continued

Table 3. (continued)

Characters	1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar
Organs on A5						
SO near spiracle bt/ SD- and L-group	present (1)	present (1)	present (1)	-	-	present (2–3)
spiracle PCO	absent	flat (1)	sunken (3)	-	-	sunken (12) and raised (22)
Organ behind D1 seta (bt/ D1–2)	PPO (1)	spherical (1)	spherical (1)	-	-	-
Organs on A6						
SO near spiracle bt/ SD- and L-group	present (1)	absent	absent	-	-	present (2)
spiracle PCO	absent	flat (1)	sunken (2–3)	-	-	sunken (19–21)
SO bt/ SD- and L-group	absent	absent or present (1)	absent	-	-	present (1)
Organ behind D1 seta (bt/ D1–2)	PPO (1)	SO (1)	SO (1)	-	-	present (4)
Organs on A7						
SO near spiracle bt/ SD- and L-group	present (1)	present (1)	present (1)	-	-	present (3–6)
spiracle PCO	absent	flat (2–3)	flat to sunken (5–6)	-	-	sunken (28–38)
organ behind D1 seta (bt/ D1–2)	PPO (1)	spherical (1)	spherical (1–2)	-	-	-
Organs on A8–9						
spiracle SO on A8	present (1)	present (2–3)	present (5–7)	-	-	present (58) (n =1)
spiracle PCO on A8	absent	absent	absent	-	-	absent
organ behind D1 seta (bt/ D1–2) on A8	absent	SO (1)	SO (2)	-	-	-
SO on A9 behind A8 spiracle SO	present (1)	absent	absent	-	-	absent
Organs on A10						
CTO on anterior-lateral of shield	absent	present (2+1 seta or 3)	present (5–6)	-	-	present (25–38)
CO on shield posterior corner (triangle zone)	present (1)	present (1)	absent	-	-	-
Organ on lateral of proleg	SO (1)	CO (1)	CO (1)	-	-	-
SO on posterior of proleg	absent	present (1)	present (3–4)	-	-	-
CO on lateral of shield	present (1) or 1 seta	absent	absent or (1)	-	-	-
Species of specimens examined	*E. chrysippe*, *E. bettina*	*E. chrysippe*	*E. bettina*	*E. chrysippe*	*E. chrysippe*	*E. chrysippe*, *E. bettina*
Number of specimens examined under SEM	n=3, n=3	n=2	n=2	(n=1) stereo-microscope	(n=1) stereo-microscope	n=2, n=2

SECOND INSTAR

Diagnosis: Head capsule width of *Euselasia chrysippe* is ca. 0.33 mm; the body is pale grayish-green without any dark spots on dorsum; and the proleg on A10 has 9–10 uniordinal crochets in a lateroseries and five crochets in mesoseries. In *E. bettina* the head capsule is wider (ca. 0.35 mm); the body color is darker, more grayish, with dorsal pinacula dark-gray to black on T2–A8; and the proleg on A10 has 11–12 uni- to biordinal crochets in a lateroseries and six uniordinal crochets in mesoseries.

Description (Figs. 25, 136–145): Differs from first instar as described and figured below (also see Table 3). Remaining instars essentially same (i.e., presence and position of setae) as second instar. Body length 2.0–2.9 mm, pale grayish-green with dull green lines dorso-longitudinally and subdorsally along segmental folds. **Head** (Figs. 136–137): Width ca. 0.33 mm, semi-translucent pale orange-brown, 1–4 extra setae in some setal groups; arrowhead setae (= more or less triangular), with short, flat, apex pointed, ridged medio-longitudinally, with cylindrical base (Figs. 136–139, Table 3), scattered on head, but more concentrated on frons, ca. as long as stemma diameter and twice as long as wide, projecting forward, apparently in pairs, i.e., in similar positions in left and right half of the head; mandible as in first instar, but with seven distinct teeth. **Thorax:** T1 (Figs. 137–139): Shield pale-orange, with eleven pairs of relatively long setae with micro-projections along anterior and lateral margins, three pairs of short slender needlelike setae with micro-projections in middle of shield, two pairs of very short setae on near lateral margin of shield, SD2 as in first instar, twelve pairs of arrowhead setae along anterior and posterior margin, and 2–3 pairs of circular tablet organs on latero-posterior margin (when circular tablet organ absent on one side, usually replaced with a seta or arrowhead setae); D1–2

thick, brown, projecting upward; 1–2 spherical organs posterior to D1–2 (position differs from first instar and sometimes replaced by a fine short seta); six pairs of semi-translucent white to pale-brown setae (XD-group and other setae) projecting forward from anterior margin, shorter and thinner than D1–2; four pairs of arrowhead setae along posterior margin (arrowhead setae sometimes replaced by fine short setae), some setae slightly spiraled apically; L-group bisetose; SV-group trisetose, spherical organ as in first instar; bladelike seta nearly as long as femur, similar to arrowhead setae but slightly larger (Fig. 139); arrowhead setae dense, projecting from ventro-subventral portion along thoracic legs (Fig. 139); spatulate-tipped setae on tarsus and tibia (Fig. 139, Tables 3–4) as in first instar. T2–T3 (Figs. 139–140): As in T1 except pale-gray dorsally; dorsum with pinacula with 6–7 setae, D1–2 as in first instar with four other semi-translucent white to pale-brown setae, thinner and shorter than D1–2 (Fig. 140), L-group with six semi-translucent white to pale-brown, somewhat featherlike setae, projecting laterally (sometimes replaced with spherical organ, e.g., Fig. 141); four spatulate-tipped setae on tibia, two on femur (Fig. 139, Tables 3–4). **Abdomen.** A1 (Fig. 140): As in T2–T3 except D-group with seven setae; D1–2 not bifurcate (Fig. 140); spiracles with a spherical organ (= spiracle spherical organ); SV area with some arrowhead setae; V-group bisetose; flat seta as in first instar, but difficult to distinguish from arrowhead setae. A2: As in A1 except a raised perforated cupola organ (PCO) similar to that described by Harvey (1987b, 1989) (i.e., lenticle dorsal to spiracle = spiracular PCO) (Fig. 141, Table 3); V-group trisetose. A3–6 (Fig. 141): As in A2 except flat spiracular PCO on A4–6; proleg with 5–7 uniordinal crochets in latero- and mesoseries, as in first instar. A7 (Fig. 141): As in A2 except 2–3 flat spiracular PCOs clustered together; SV seta, short spinelike laterally contiguous to flat seta. A8–9 (Figs. 142, 145): Dorsal and subdorsal portions of A8 as in A7 except spiracular PCOs absent; 2–3 spiracular spherical organs posterior to spiracle; SD-group absent. Dorsal and subdorsal portions of A9 with D- and SD-group absent as in first instar; spherical organ posterior to A8 spiracular spherical organ absent (Table 3). Lateral portions of A8+9 with L-group of eleven setae. Subventral and ventral portions of A8–9 as in A2. A10 (Figs. 142–145): anal plate (Fig. 143) with six brown thick setae projecting dorso-caudally along with other slender, long or short setae, 2–4 circular tablet organs on each side of anterior margin (circular tablet organs sometimes absent on one side and replaced with seta) (Fig. 143, Table 3), cupola organ on each latero-posterior margins (Fig. 144, Table 3); eight claw-shaped setae as in first instar (Fig. 145, Table 3), a few thick, setae posterior and anterior to claw-shaped setae; proleg with two spherical organs, on lateral pinaculum and posterior end respectively; 9–10 uniordinal crochets in semicircular lateroseries and five uniordinal crochets in mesoseries.

Material examined: Lake Arenal, 2003 (SEM, n = 2; dissecting stereo-microscope, n = 1).

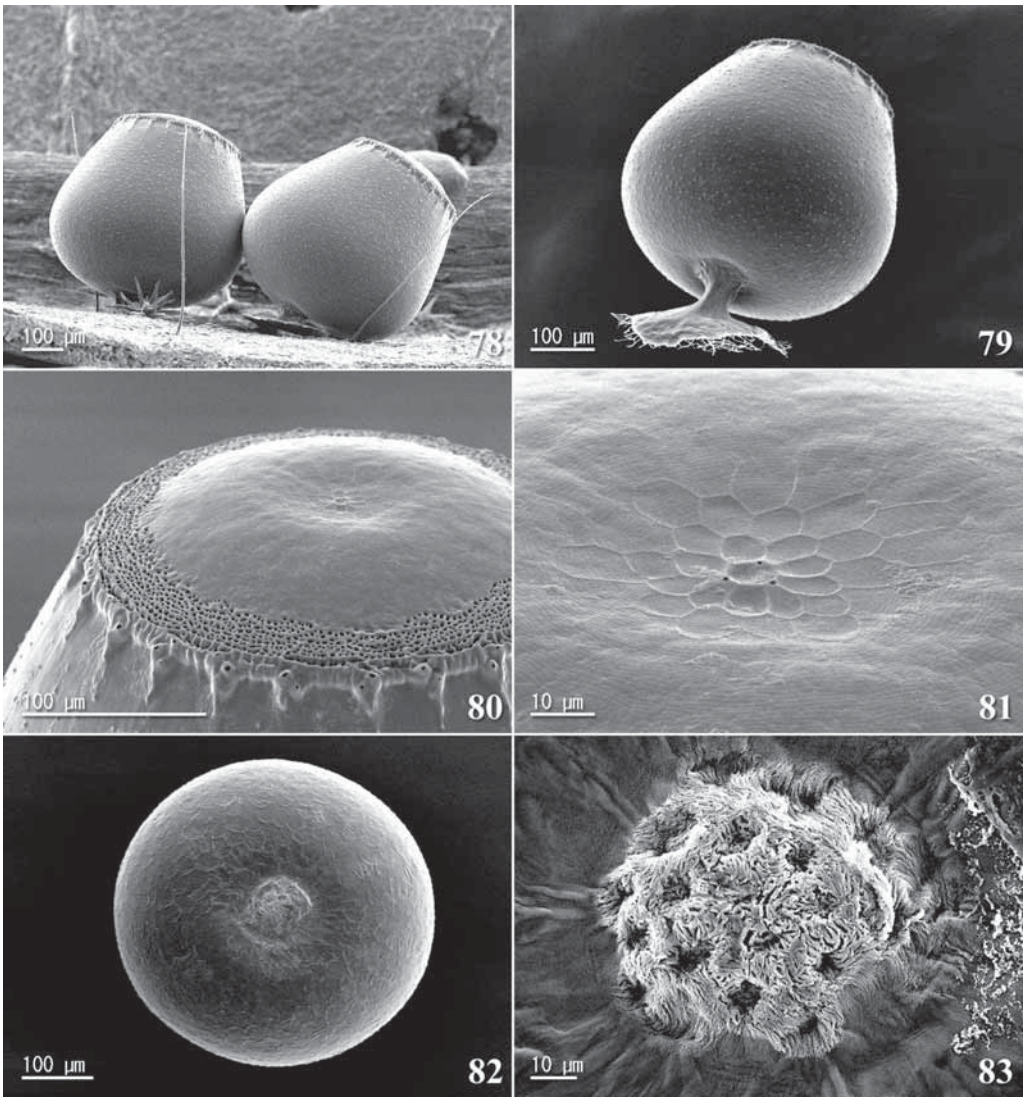
TABLE 4. Number of spatulate-tipped setae in mesal portion of each thoracic leg segment of larval *Euselasia*. (n = 3 each).

Specimens	Tarsas	Tibia	Femur	Coxa
E. chrysippe / *E. bettina* first instar T1	2	0	0	0
E. chrysippe / *E. bettina* first instar T2	2	2	0	0
E. chrysippe / *E. bettina* first instar T3	2	2	0	0
E. chrysippe second instar T1	2	2	0	0
E. chrysippe second instar T2	2	4	2	0
E. chrysippe second instar T3	2	4	2	0
E. bettina third instar T1	2	2	0	0
E. bettina third instar T2	2	4–6	3	0
E. bettina third instar T3	2	5	4–5	0
E. chrysippe sixth instar T1	2	3	0	0
E. chrysippe sixth instar T2	2	9–11	11–12	0
E. chrysippe sixth instar T3	2	10–14	11–13	0

THIRD INSTAR

Diagnosis: The head capsule width of *Euselasia chrysippe* is ca. 0.53 mm; the overall body color is greenish-pale-gray; the T1 shield is pale-orange; the color of the dorsal pinacula on T2–A8 is gray becoming faint in posterior segments; the mesal line and intersegmental membrane are dull green; the anal plate is pale-gray; the proleg on A10 has 6–7 crochets in mesoseries. Head capsule width of *E. bettina* is slightly wider, ca. 0.55 mm; the overall body color is darker (gray); the T1 shield has a pair of black transverse lines; the dorsal pinacula of T2–A8 are prominent black; the mesal line, intersegmental membrane, and anal plate are black; and the proleg on A10 has more crochets (8–9) than *E. chrysippe*.

Description (Figs. 26–27, 30, 148): Similar to previous instar except for the following. Body length 2.8–5.0 mm, overall color greenishi-pale-gray. **Head**: Width ca. 0.53 mm, orange; more secondary setae in each setal group and more arrowhead setae compared to previous instar (this tendency continues in remaining instars); mandible (Fig. 148) somewhat palmate, with seven small, distinctly dentate teeth, inner surface concave.

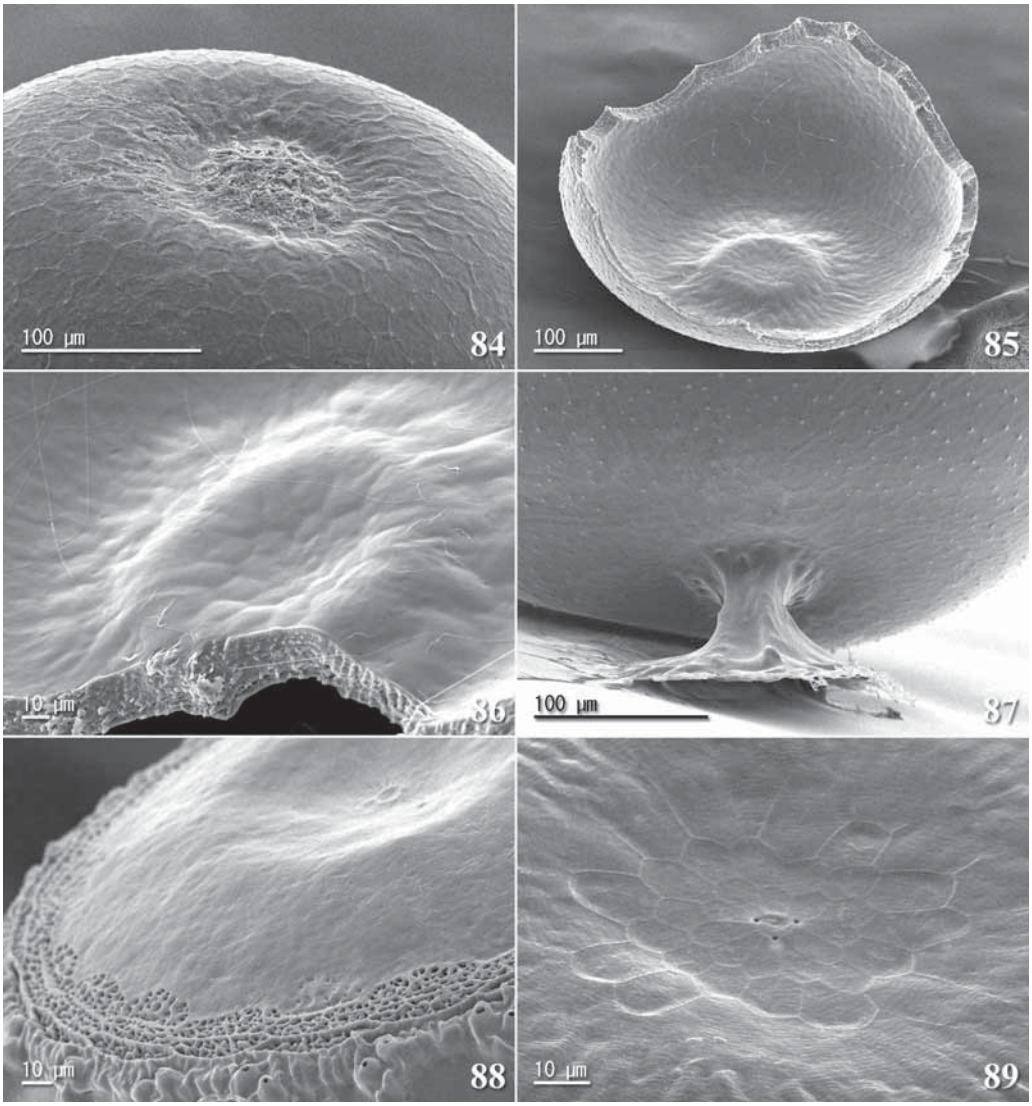


FIGURES 78–83. SEM of egg of *E. chrysippe*. **78)** Lateral view, in situ (note stellate trichomes of host leaf); **79)** Latero-ventral view, showing stalk; **80)** Apical rim and micropyle area, dorso-lateral view; **81)** Micropyles and rosette, dorso-lateral view; **82)** Stalk conjunctional structure in the center, ventral view, stalk removed; **83)** Stalk conjunctional structure, ventral view, (remnants of stalk seen as white).

Thorax and abdomen. T1: whitish-pale-orange. T2–A8: Pinacula on dorsum gray and faint in posterior segments (presence and level of gray varied between larvae within a group); lateral lobes semi-translucent

pale-brown; a faint whitish-pale-gray longitudinal line subdorsally along lateral lobes; prolegs with 7–12 uniordinal crochets in lateroseries and 18–21 weakly biordinal crochets in mesoseries. A9: Dorsally and subdorsally as in second instar except a short, slender SD seta in mid-subdorsum. A10: Anal plate pale-gray (opaque); proleg with crochets weakly biordinal, 13–14 in semicircular lateroseries and 6–7 uniordinal crochets in mesoseries.

Material examined: Lake Arenal, 2003 (dissecting stereo-microscope, n = 1); La Selva, 2007 (dissecting stereo-microscope, n = 1).



FIGURES 84–89. SEM of egg of *Euselasia*. **84)** Stalk conjunctional structure (stalk removed) and hexagonally arranged sculpturing of chorion, ventro-lateral view (*E. bettina*); **85)** Concave structure at center part of ventral inner surface (opposite surface of stalk conjunctional structure), dorso-lateral view (*E. bettina*); **86)** Concave structure (*E. bettina*) (white narrow lines = silk); **87)** Stalk, lateral view (*E. bettina*); **88)** Apical rim and micropyle area (*E. bettina*), dorso-lateral view; **89)** Micropyles and rosette (*E. bettina*), dorso-lateral view.

FOURTH INSTAR

Diagnosis: Overall body color of *Euselasia chrysippe* is grayish-green; the head capsule width is ca. 0.72 mm; the color of the T1 shield is mostly orange; the pinacula on dorsum are dull black; the mesal line and intersegmental membrane are dull green; the A10 proleg has 20–22 biordinal crochets in lateroseries. Overall body color of *E. bettina* is grayish-yellow; the head capsule is slightly wider (ca. 0.80 mm); the T1 shield is mostly black; the pinacula on dorsum are darker, in prominent black; mesal line and intersegmental membrane are dark-green; and the proleg on A10 has more crochets (25–26).

Description (Figs. 28–30, 149): Similar to previous instar except as described below. Body length 5.2–8.6 mm; overall color slightly more grayish and greenish dorsally compared to third instar; mesal line and intersegmental membrane dull green. **Head**: Width ca. 0.72 mm, bright orange; mandible (Fig. 149) with distal area laterally widened and straight, with five indistinct teeth, inner surface more concave and steeply angled than previous instars. **Thorax and abdomen.** T1: Shield orange, posterior ca. one-fourth with a pair of narrow, dull black, transverse lines, with three pairs of dark-brown setae projecting dorsally and several semi-translucent white to pale-brown, slender setae projecting over head from anterior margin; 9–10 circular tablet organ in posterior-lateral margin (Table 3); L-group with 8–10 long setae, SV-group with 8–10 long setae. T2–A8: Dorsum with dull black pinacula with a dark-brown to semi-translucent brown seta and several semi-translucent pale-brown to white setae projecting dorsally; proleg with 13–16 biordinal crochets in each row. A9: Dorsally and subdorsally as in previous instar. A10: Anal plate with a pair of dark-gray to black transverse arch-shaped lines, with four pairs of thick, dark-brown setae and several semi-translucent pale-brown to white thinner setae projecting dorsally to caudally, with semi-translucent white, slender, featherlike setae along latero-posterior margins; circular tablet organ (Table 3); space between arch (medio-posterior portion) whitish; proleg with 20–22 biordinal crochets in lateroseries in semicircle and 11–12 biordinal crochets in mesoseries.

Material examined: Lake Arenal, 2003 (dissecting stereo-microscope, n = 3).

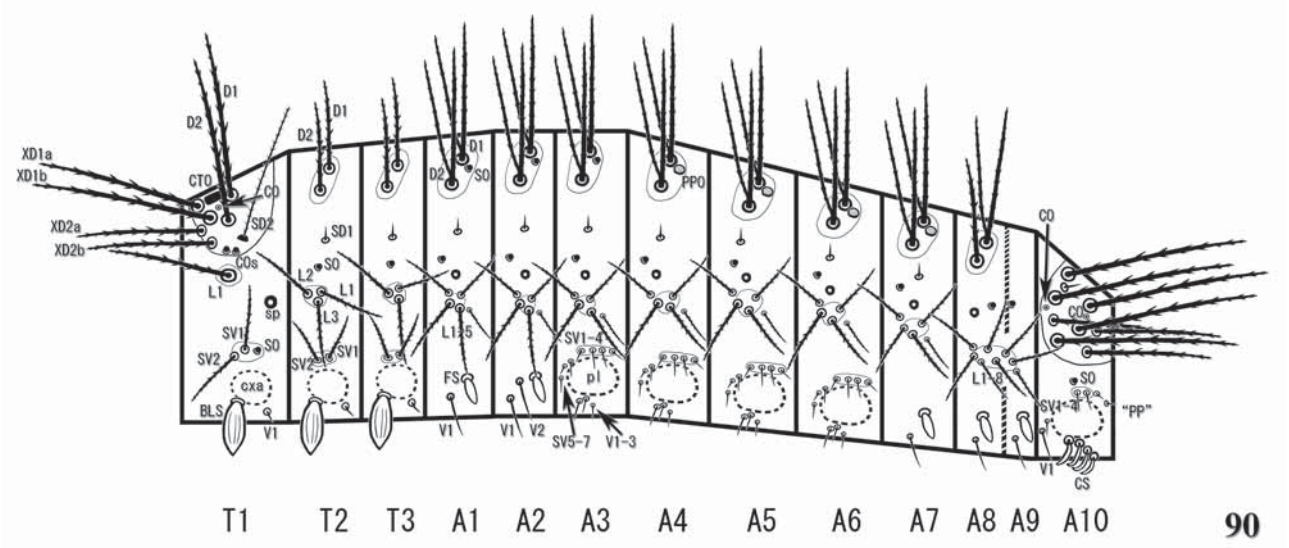


FIGURE 90. Chaetotaxy of first instar larva of *Euselasia chrysippe* and *E. bettina* (lateral view). CO = cupola organ, CS = claw-shaped setae, CTO = circular tablet organ, cxa = coax, pl = proleg, "PP" = "proprioceptor" seta, PPO = perforated plate organ, SO = spherical organ.

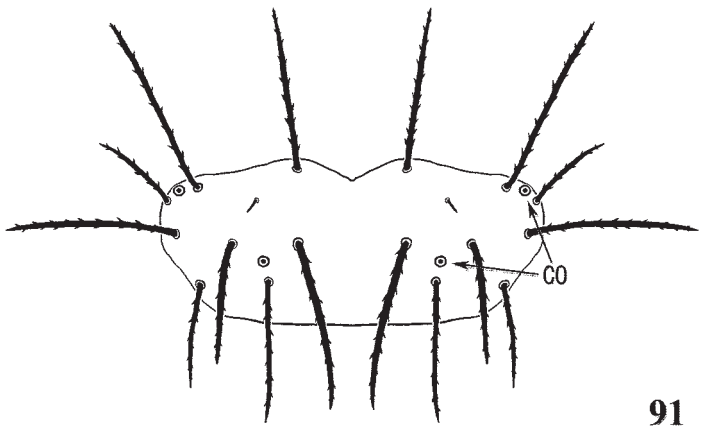
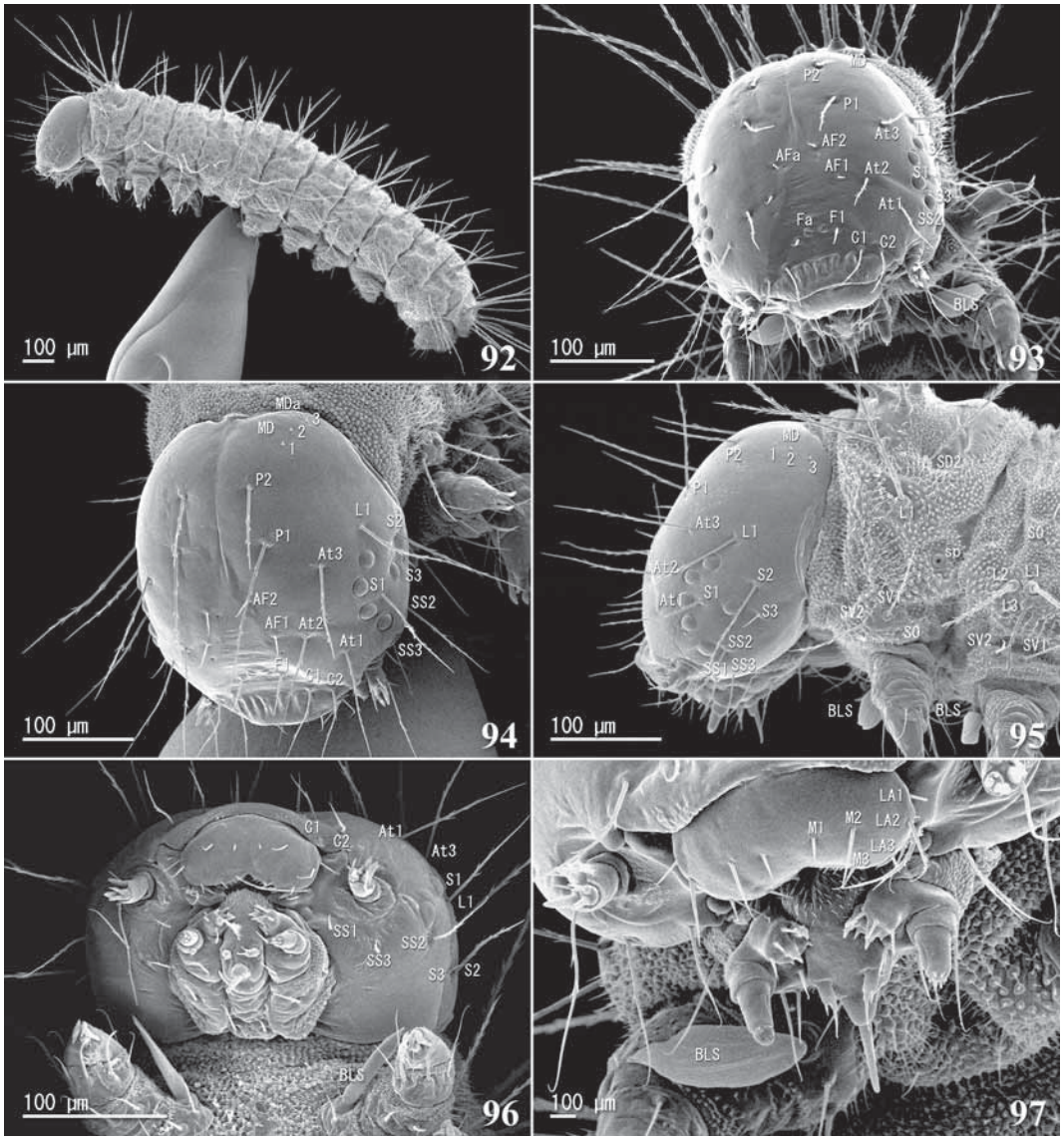


FIGURE 91. Chaetotaxy of anal plate of first instar larva of *Euselasia chrysippe* and *E. bettina* (caudal view). CO = cupola organ.

FIFTH INSTAR

Diagnosis: The fifth instar *Euselasia chrysippe* is gray to yellowish-gray; the head capsule width is ca. 1.23 mm; the T1 shield is mostly orange; and the proleg on A10 has 11–13 crochets in a mesoseries. *E. bettina* is greenish-black to greenish-dull yellow; the head capsule width is slightly wider (ca. 1.30 mm); the T1 shield is entirely black or mostly black with little orange; and.A10 has more crochets (15–16).

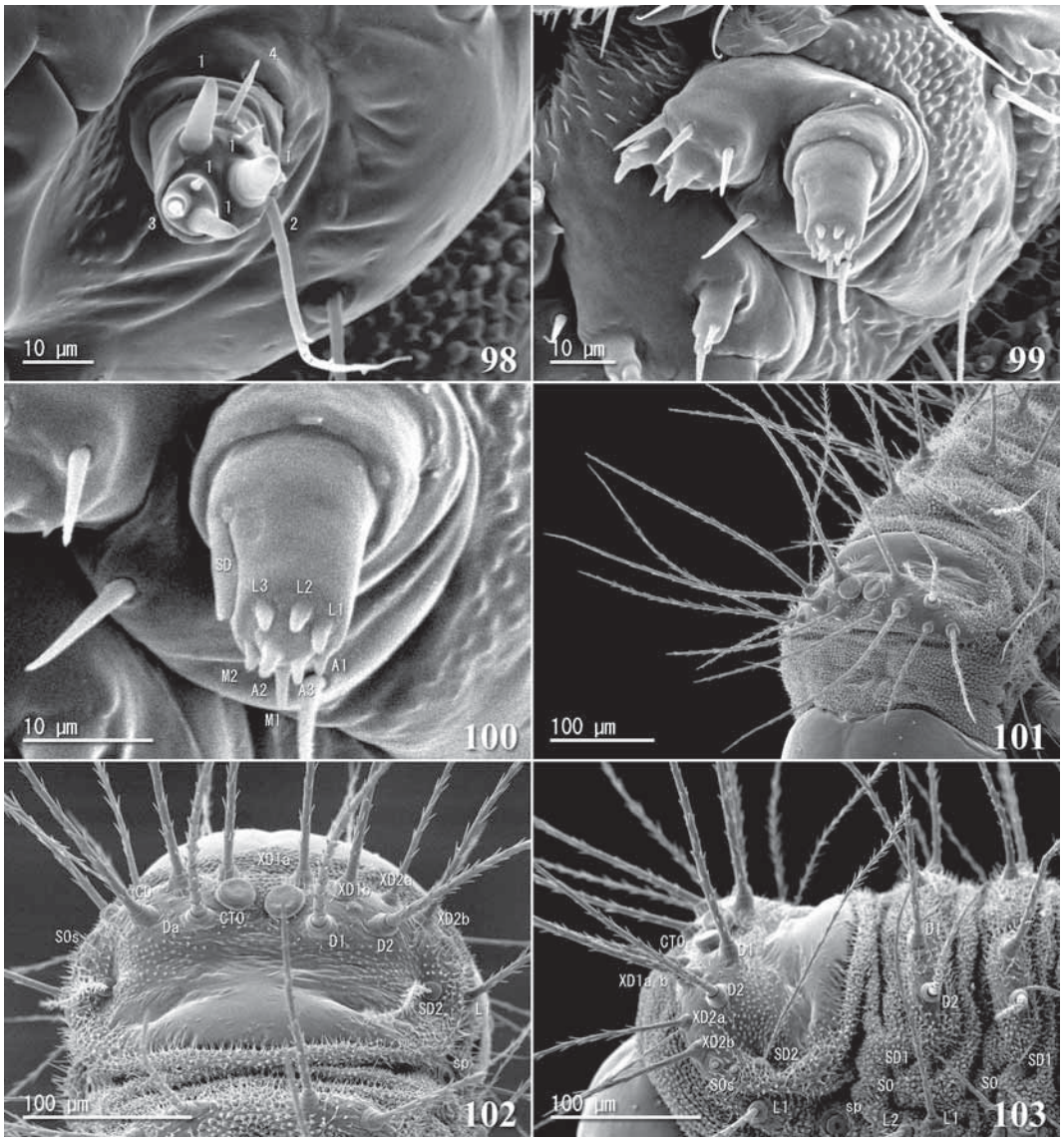


FIGURES 92–97. SEM of *Euselasia* first instar larva. **92)** Lateral view (*E. bettina*); **93)** Head, frontal view, (*E. chrysippe*); **94)** Head and cervical area, dorso- lateral view (*E. chrysippe*); **95)** Head and T1–2, lateral view (*E. bettina*); **96)** Head and T1, ventral view (*E. chrysippe*); **97)** Mouthparts, frontal view (*E. chrysippe*).

Description (Figs. 31–32, 68): Similar to previous instar except as described below. Body length 9.0–13.2 mm, overall color gray to yellowish-gray, lateral lobes slightly more protuberent; minute semi-translucent white to pale-brown, short, hairlike setae sparsely throughout body surface (at 32X). **Head**: Wdith ca. 1.23 mm, orange to dark-brown (Fig. 31) or bright orange (Fig. 32). **Thorax and abdomen.** T1: Shield bright to dull orange, with a pair of dark-brown patches in posterior one-fourth to one-half, 3–4 pairs of prominent dark-brown setae projected dorsally and subdorsally along with a few semi-translucent white slender setae projecting over head; circular tablet organ lenslike, i.e., translucent or colorless (Table 3); L-group with 10–12 long setae; SV-group with 10–12 long setae. T2–A8: Pinacula on dorsum black with two dark-brown setae along with several semi-translucent pale-brown to white slender setae projecting dorsally; proleg with 18–21 biordinal crochets in each row. A9: Dorsally and subdorsally as in previous instar except SD bisetose. A10:

Anal plate arched, with 8–10 dark-brown setae and with several slender semi-translucent white to pale-brown setae projecting latero-caudally; circular tablet organ (see Table 3); space between arch (posterior middle part) white; proleg with 28–33 biordinal crochets in semicircular lateroseries and 11–13 biordinal crochets in mesoseries.

Material examined: Lake Arenal, 2003 (dissecting stereo-microscope, n = 3).

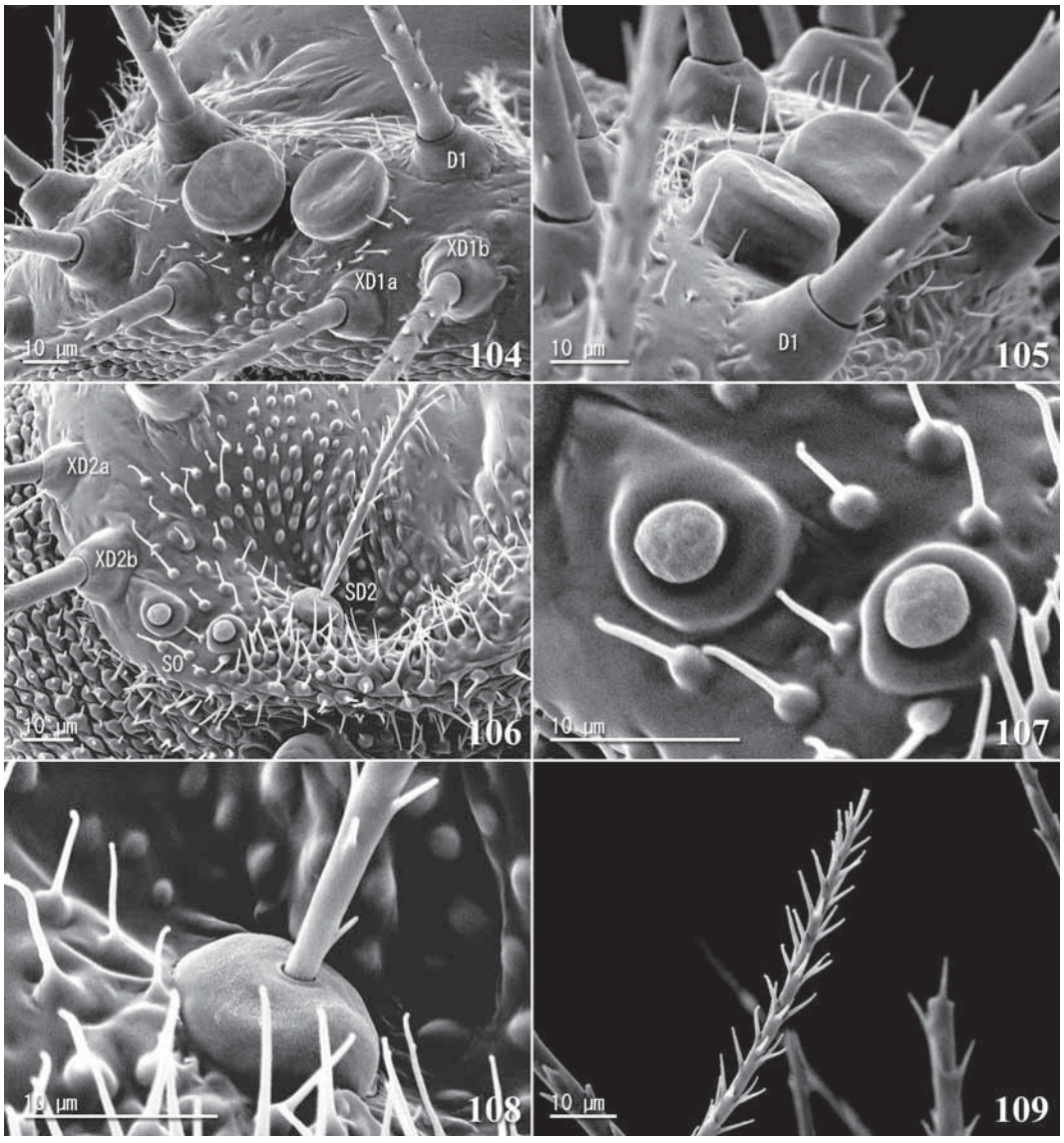


FIGURES 98–103. SEM of *Euselasia* first instar (*E. chrysippe*). **98)** Left antenna showing arrangement of sensilla, frontal view; **99)** Left galea showing lobe of galea and maxillary palpus, dorso-frontal view; **100)** Maxillary palpus and sensilla arrangement, dorso-frontal view; **101)** Head and T1–3, dorso-frontal view; **102)** T1 shield, dorsal view; **103)** T1–3, dorso-lateral view.

SIXTH INSTAR

Diagnosis: The sixth instar *Euselasia chrysippe* is greenish-dark-gray to greenish-dull black; the head capsule width is ca. 1.65 mm; the color of the head is bright orange, black, or a mixture of these two; arrowhead setae are cone-shaped (not flattened), ridged, and spiraled apically; the curvature of the ventral margin of the labrum is narrowly angled (ca. 110°); the mandible is small (0.38 mm wide), with the dentation less distinct than in *E. b*ettina, and the extension of the fifth tooth is somewhat widened at edge; the T1 shield is orange to bright orange and without iridescence; the pinacula on the dorsum have a pale-gray oval line; the iridescence on structural color plates is faint metallic-blue; a proleg on A10 has 11–13 crochets in mesoseries. *E. bettina* sixth instar is brownish-amber with reddish or greenish tint; and head is slightly wider (ca. 1.75 mm) and

black with a pair of brownish-orange to pale-orange patches running parallel to epicranial suture; the arrowhead setae are flattened' the curvature of the ventral margin of labrum is more widely angled (ca. 120°); the mandible is larger (ca. 0.45 mm wide) and dentation is slightly more distinct; the T1 shield is bright orange with reddish tint, and black transverse lines have faint bluish-gray iridescence; the pinacula on the dorsum are black with a white oval line; the iridescence of the structural color plates is brighter and metallic sky-blue; and the proleg on A10 has more crochets in mesoseries (15–16) than in *E. chrysippe*.



FIGURES 104–109. SEM of *Euselasia* first instar (*E. chrysippe*). **104)** Paired circular tablet organs on medio-anterior part of T1 shield, dorso-frontal view; **105)** Circular tablet organ, lateral view; **106)** T1 shield showing spherical organs (SOs) and SD2, dorso-lateral view; **107)** Spherical organs; **108)** Pinaculum of SD2; **109)** Middle to apical area of SD2, lateral view.

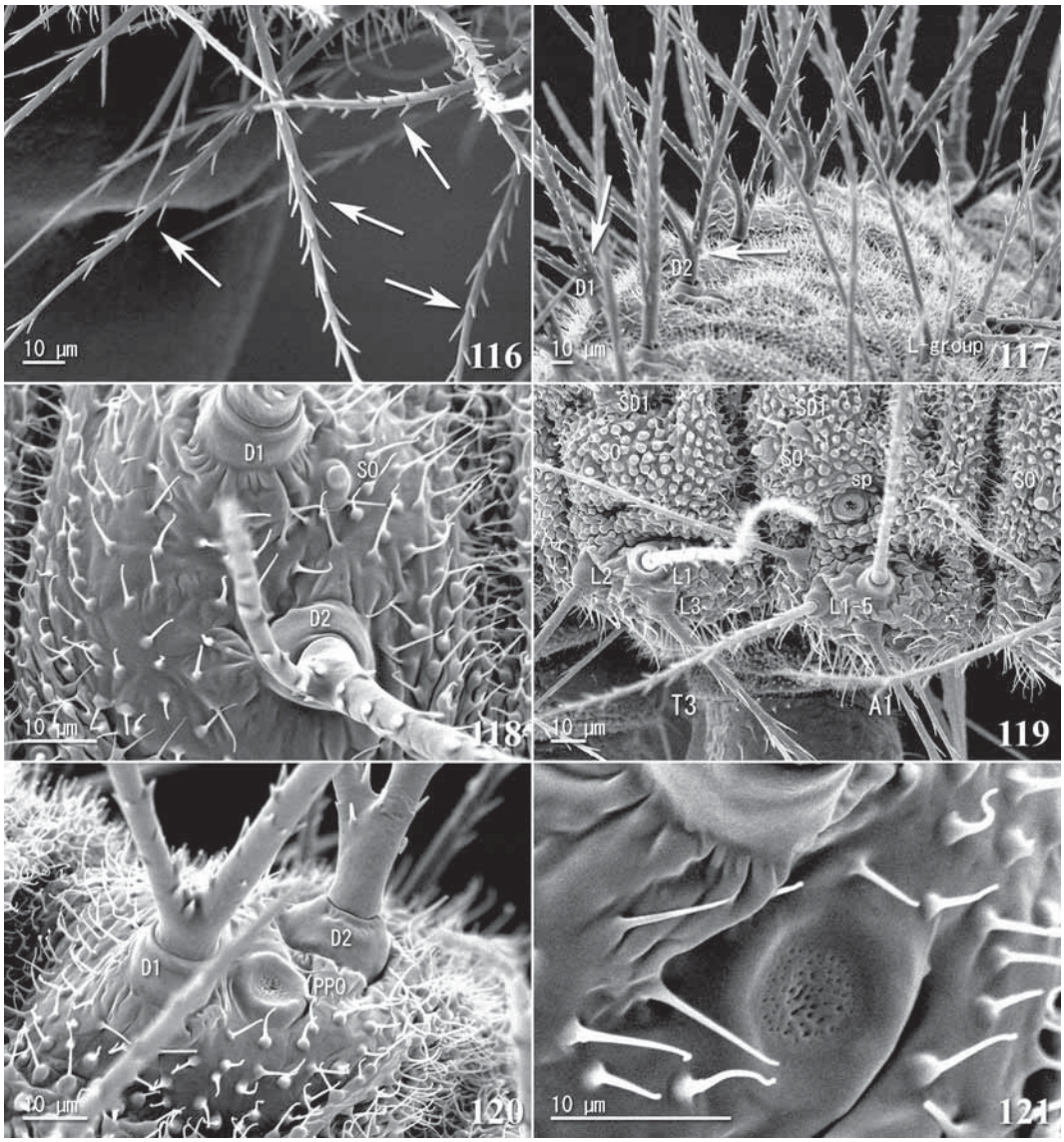
Description (Figs. 33–39, 42–44, 150, 152–156, 159, 161, 163, 168–194, 196–207): Similar to previous instar except as described below. Body length 12.8–19.0 mm, overall color greenish-dark-gray to greenish-dull black (Figs. 33–34, 36–37, 43–44), distinct from of other instars; spherical organs scattered sparsely on body, more concentrated near spiracles, SV pinacula, and on anal plate near circular tablet organ (Figs. 183, 186, 188, 204). **Head** (Figs. 34–35, 43, 152–154): Width ca. 1.65 mm, bright orange (Figs. 34–35, 37), black (Figs. 39, 43), or mixture of these two (Figs. 34, 44); cuticle of head capsule semi-translucent pale-brown to dark-brown; arrowhead setae semi-translucent with slight brownish tint (Figs. 34–35), most cone-shaped (not flattened), ridged, and spiraled apically (i.e., shape differs from those of second instar) (Figs. 161, 163),

densely scattered over head, more so on frons, stemmatal area, and oral area (Figs. 152–156, 183); more sparsely scattered on other parts of body; each setal group with numerous setae; labrum as figured (Figs. 155, 159), curvature of ventral margin widely angled (ca. 120°); mandible (Fig. 150) 0.38 mm wide, distally more widened and straight, with five indistinct teeth, edge of tooth farthest from condyle straight and continuous (n = 5); sensilla of antenna and maxillary palpus as figured (Figs. 169–170). **Thorax.** T1 (Figs. 33–35, 37, 43–44, 171–176): Shield orange to bright orange on anterior half, posterior half with a pair of black transverse lines and posterior-lateral margins with a whitish line on each side (Figs. 33–35); six pairs of stout, dark-brown to black setae with microprojections dorsally and dorso-laterally (Figs. 34–35, 43–44, 171), three setae on orange anterior portion, one on orange lateral portion, and two on white posterior portion; six pairs of semi-translucent pale-brown to white, long, slender setae projecting over head from anterior portion to subdorsal portion of shield with several other short, semi-translucent white to pale-brown slender setae; SD2 (Figs. 43, 171–175) semi-translucent white to pale brown, length ca. one-half that of stout setae, with microprojections on shield, loosely socketed; circular tablet organ (Fig. 172, Table 3) ca. 22 μm in diameter, translucent or with brownish tint, porelike structure in inner center; L-group with ca. 15 setae projected laterally, long setae about as long as body width, short setae ca. one-third length of long setae, semi-translucent white to pale-brown setae with micro-projections; SV-group (Fig. 183) with >10 semi-translucent pale-brown slender setae of various lengths (<0.4 mm) projecting laterally; bladelike seta (Fig. 182, Table 3) on legs, straight, basal half cylindrical, apical half flat with pointed tip; spatulate-tipped setae (Figs. 176–181, Tables 3–4) slightly longer than each leg segment, colorless semi-translucent (in both live and preserved specimens), spatulate-tip ventrally with irregular narrow grooves (Figs. 177–179) and some with small oval "windows" (Fig. 178), dorsally with longitudinal ridges more or less along entire seta (Fig. 180); spatulate-tipped setae on femur commonly with sharply pointed apex (Fig. 181). T2–T3 (Figs. 33–34, 43–44, 196): Pinaculum on dorsum (Fig. 196) blackish and slightly greenish, with a pale-gray semi-oval area in middle; D-group with three dark-brown to black stout setae with microprojections with approximately 8–10 semi-translucent white to pale-brown setae projecting dorsally; structural color plate on anterior subdorsum of black pinaculum, with faint metallic-blue iridescence (Figs. 36, 43), also present on abdominal segments (Figs. 195–197, 199–201); anterior subdorsum of color plate with two slender semi-translucent white to pale-brown setae; black-colored area densely covered by microtrichia (Figs. 196–197); structural color plate concave and contiguous to tonofibrillary platelets (Fig. 199), with sparsely scattered microtrichia; anterior part of plate with two slender semi-translucent white to pale-brown setae projected forward; L-group projecting in two layers with two types of semi-translucent white to pale-brown setae (Figs. 192–194), one above longer (ca. two-thirds of body width) with micro-projections (ca. 10 setae), and the other shorter and featherlike (ca. 30), projected along lateral lobes; SV-group with ca. 10 long semi-translucent pale-brown setae and other short setae. **Abdomen.** A1–2 (Figs. 33, 44): Structural color plate larger than on T2; dorsal pinaculum with 3–4 dark-brown to black stout setae with microprojections along with 6–7 semi-translucent pale-brown to white setae; SV-group with one long, slender seta with micro-projections, V-group with 5–8 setae (A2 with more setae), one mesally located longer than others, flat seta absent. A3–6 (Figs. 33, 36, 44, 184–185, 191, 197, 206): Similar to A1–2 except dorsal pinaculum with four dark-brown to black stout setae with microprojections (Fig. 191) with seven semi-translucent white to pale-brown setae; structural color plate with two setae on anterior part, one on middle, and two on posterior part; longitudinal white line subdorsally along spiracles between dorsal pinacula and lateral lobes (through A3–9); lateral lobes semi-translucent dull white; spiracular PCOs (Figs. 184–187, Table 3) surrounding spiracles, more cephalad and dorsally to spiracle; PCOs translucent (in live and preserved specimens), raised, flat, sunken; proleg with 18–21 biordinal crochets in each series. A7 (Figs. 33, 36, 206): D-group with 5–6 dark-brown to black stout setae with microprojections and approximately 6–7 semi-translucent white to pale-brown slender setae projecting dorsally; subdorsally as in A3–6; ventrally as in A1 except V-group with 2–3 setae, one located mesally as long as proleg on A6. A8-9: Dorsal and subdorsal portion of A8 (Figs. 33, 44) similar to A7 except subdorsum of anterior part of color plate with 1–2 semi-translucent white to pale-brown slender seta; longitudinal white line prominently white and broader than in other segments, with spiracle in center; spiracular spherical organs as figured (Figs. 188–190, Table 3). Dorsal and subdorsal portions of A9 (Figs. 33–34, 43–44, 202–203)

similar to that of previous instar (unable to distinguish SD setae from minute setae in D and SD area). Subventral and ventral portions of A8 (Fig. 206) as in A7 except V-group with two setae. Subventral and ventral portions of A9 (Fig. 206) with SV absent. A10 (Figs. 33–34, 42–44, 202– 207): Anal plate and surrounding area as in previous instar except anal plate with faint metallic-blue iridescence, 11-12 dark-brown to black stout setae with microprojections and 5–7 semi-translucent white to pale-brown long setae projecting dorsally to caudally; ca. 10 brown to dark-brown long, slender setae numerous shorter featherlike semi-translucent white to pale-brown setae projecting posterio-laterally from lateral to posterior margins of plate (Figs. 42, 44, 202–203); circular tablet organ (Figs. 203–205, Table 3) same shape as in T1; claw-shaped setae (Figs. 206–207) as short as other slender setae on A10 venter, 13.5 μm thick, i.e., more slender than in previous instars, semi-translucent white to pale-brown, 33–36 on posterior middle portion, surrounded by slightly more slender setae; when expanded in procession, convex with a small semi-translucent circular spot in middle between prolegs (Figs. 206–207); proleg with 28–33 biordinal crochets in semicircular lateroseries and 11–13 biordinal crochets in mesoseries.

Material examined: Lake Arenal, 2003 (SEM, n = 2; dissecting stereo-microscope, n = 5).

FIGURES 110–115. SEM of *Euselasia* first instar. **110)** T1, lateral view, (*E. chrysippe*); **111)** Left thoracic legs, bladelike seta (BLS) and spatulate-tipped setae (STS), ventral view (*E. chrysippe*); **112)** Bladelike seta on left T1 leg, ventral view (*E. chrysippe*); **113)** Bladelike seta on left T1 leg, frontal view (*E. bettina*); **114)** Bladelike seta on left T1 leg, ventro-caudal view (*E. chrysippe*); **115)** Spatulate-tipped setae on tarsus and tibia of left T2 leg, posterior view (*E. chrysippe*).



FIGURES 116–121. SEM of *Euselasia* first instar (*E. chrysippe*). **116)** L-group setae (arrows) on right side of A2–4, dorsal view; **117)** Left side of abdominal segments showing bifurcate D1–2 (arrows), fronto-lateral view; **118)** Bifurcate D2 on left A1 and spherical organ (SO) behind D1, dorsal view; **119)** SD and L-group and spherical organ (SO) on T3–A2, lateral view; **120)** Bifurcate D1–2 and perforated plate organ (PPO) behind D1 on right side A7, dorso-lateral view; **121)** Perforated plate organ on left side A7, dorso-lateral view.

PREPUPA

Diagnosis: The prepupa of *Euselasia chrysippe* is dark brownish-gray with pale-brown. *E. bettina* is amber with black.

Description (Fig. 45): Length 11.5–12.8 mm; dorsum dark brownish-gray (slightly greenish) with pale-brown lines mesally and on pinacula, pale-brown laterally, faint metallic-blue iridescence on structural color plates observed during prepupal stage.

Material examined: Lake Arenal, 2003 (n = 30).

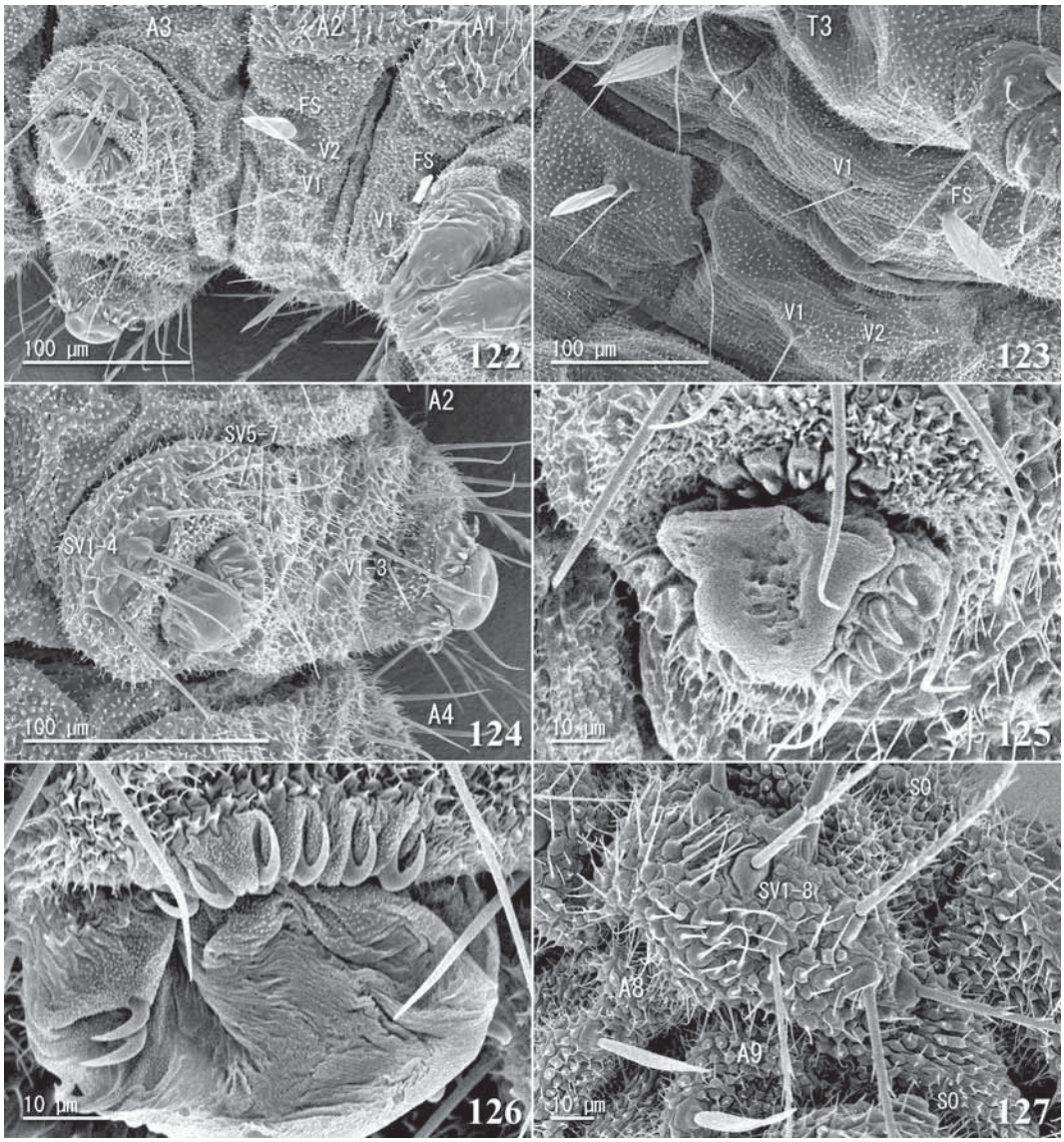
PUPA

Diagnosis: The pupa of *Euselasia chrysippe* is 11.5–12.0 mm long and 5.0–5.5 mm wide. That of *E. bettina* is usually longer and wider, 11.4–13.5 mm long, 5.7–6.4 mm wide.

Description (Figs. 6, 46–50, 208–225, Table 5): Width 5.0–5.5 mm, length 11.5–12.0 mm, and dorso-ventrally ca. 3.0 mm tall; dorsally convex, middle widened, caudally tapered, ventrally flattened; pale-creamy

yellow to brown with brown to dark-brown patches; (approximately 12 hours prior to adult eclosion the pupa becomes reddish dark-brown); cuticle with narrowly crenulate sculpturing (e.g., Figs. 208, 214) on dorsal and lateral surfaces except in following locations: subdorsal triangular zone (Fig. 208) on T3 next to A1, middle area of wing sclerites below triangular zone; cuticle more roughly sculptured on darkly pigmented areas; cuticle ventrally smooth except: outer one-third of eye piece, basal portion of antenna, pro- and T2 legs, proboscis, middle to apical area of wing sclerite; mouth parts as figured (Fig. 210), with wide clypeus and broad mandibles (some specimens with narrower clypeus and mandibles as in Fig. 211); eye piece with three distinct longitudinal linear parts (Fig. 209); inner part of center portion convex, middle part and inner part forming convex curve together; in some specimens middle part with a notch at posterior end (Fig. 211); outer part concave with narrowly crenulate sculpturing; antenna extending slightly beyond wing sclerite, extending to posterior margin of A4; proboscis extending ca. 1.5 times as long as adjacent T1 leg, slightly narrowed at middle portion of prothoracic leg sclerite widened at border of T2 leg sclerite; T2 leg adjacent to eye piece extending to wide posterior portion of proboscis; anterior end of area between head and T1 with a smoothly curved notch; thorax broadly rounded, T2 tallest; posterior end of A1–A7 dorsally flattened, gradually tapered caudally, A3 widest; thoracic spiracle (Figs. 208, 212–213) on dorsum of lateral edge between T1–2; thoracic spiracle sculpturing on anterior dorsum of T1 pale-brown with platelike bases with spines projected forwards, inner side of T1 to posterior part of T2 black with cone-shaped spines of varying size (Fig. 213); abdominal spiracles white to pale-brown, oval, slightly protuberant spiracles on A2–3 located subdorsally, spiracles on A4–7 lateral, spiracles absent on A8+9 (six in total); clubbed setae (Figs. 46–50, 76–77, 208–209, 214–219, 222–224) on dorsum 1.0–1.5 mm long, nearly as long as A4, brown, on subdorsum to lateral area thinner and paler; slender pale-brown setae, 1.0–2.0 mm long, on lateral and subventral margins of T1, T3, and A2–8+9, and dorsum to subdorsum of A10, of posterior end of T1 through of A4; number, location, and type of setae indicated in Table 5; brown to pale-brown fine short hairlike setae (Figs. 214–215, 219, 222–224) scattered more or less throughout body; clubbed setae and slender setae with longitudinal shallow ridges, with fine, short, needlelike ridged and spiraled spine projections throughout seta; spines more dense near apex (Figs. 216–218), with cuticular ring base raised (short broad cone = chalazae), apparently not socketed, i.e., continuous (Figs. 214–215, 219, 224); surface of broad cone near cuticular ring rough (Figs. 215, 219); basal area of clubbed setae wider than apical area immediately below clubbed apex; apex of clubbed setae composed of densely grouped, ridged and spiraled setae on slightly swollen setal tip (Figs. 217–218); silk-clipper (a structure which sustain silk girdle) on mid-dorsum of A1 (Fig. 214), mid-dorsum of A1 with a narrow transverse groove, a pair of narrow 'clips' projecting from anterior end of groove, a broad "clip" projecting from posterior of groove between narrow "clips" (see Dias Filho 1980); intersegmental membrane between A4 and A5, A5 and A6, and A6 and A7 (Figs. 208–209, 219) widely exposed from subdorsal to lateral; lateral portion of outer surface intersegmental membrane in anterior A5–7 with spinose sculpturing (Fig. 220) and lateral portion of inner surface intersegmental membrane in posterior A4–A6 with transversely ridged sculpturing (Fig. 221) (similar to 'tooth-cast' system *sensu* Downey & Allyn 1973); notch between head and T1 dark-brown; posterior edge of T1 with a brown to dark-brown transverse line; posterior region of thoracic spiracle dark-brown to black; latero-anterior margin of tallest ovoid area of T2 with a dark-brown transverse line; dorsum of middle posterior portion of T2 dark-brown; cuticular ring base of eight clubbed setae on mid-dorsum of T2 dark-brown; subdorsal triangular zone on T3 next to A1 dark-brown; lateral side of wing sclerite margin dark-brown; wing sclerite with 2–3 longitudinal dark-brown stripes laterally; between dorsal setae on A2–3 with a pair of dark-brown areas and pale whitish-brown area; A4 mostly dark-brown; A5–7 dorsally dark-brown, subdorsally pale whitish-brown; raised cuticular ring bases on dorsum of A5–7 black; dorsum of A8+9 black; A10 dorsally black, subdorsally pale whitish-brown; cremaster consisting of semi-translucent pale-brown, double-hooked spines (Fig. 225), lined along ventral folds of A10 (forming V-shape) and continued to surround posterior end of A10 (Figs. 222–224); pupal shell semi-translucent pale brown to reddish pale brown (Fig. 6).

Material examined: Lake Arenal, 2003 (SEM, n = 2 complete specimens and 2 exuviae; dissecting stereo-microscope, n = 3 complete specimens and 10 exuviae).



FIGURES 122–127. SEM of *Euselasia* first instar. **122)** Flat setae (FS) and prolegs, ventro-lateral view (*E. chrysippe*); **123)** Flat seta (FS) and V-group on T3–A2, ventral view (*E. bettina*); **124)** Prolegs and SV-group on A3, ventro-lateral view (*E. chrysippe*); **125)** Arrangement of crochets on right side of A5 proleg, ventral view, lateroseries on top (*E. chrysippe*); **126)** Crochets on left side of A5 proleg, ventro-lateral view, lateroseries on top (*E. chrysippe*); **127)** L-group, flat setae, and spherical organ (SO) on left side A8+9, and spherical organ (SO) on A10 proleg, ventral view (*E. chrysippe*).

Diagnosis and description of early stages of *Euselasia bettina*

EGG

Diagnosis: The egg of *Euselasia bettina* is opaque (creamy-white), 0.45 mm in diameter. Pigmentation of the lateral wall extends beyond the apical rim, up to ca. one-sixth egg height. The width of the crenulated rim is ca. one-seventh of the dorsal surface diameter. The apical rim is purplish- brown. The rosette of the third row has a few closed cells. The egg of *E. chrysippe* is semi-translucent pale-brown and slightly smaller (0.42 mm diameter), with wider pigmentation, extending beyond apical rim to ca. one-third of egg height, and the width of the crenulated rim area is wider, ca. one-fifth of dorsal surface diameter. The apical rim is purplish-dark-brown. The rosette of the third row has no closed cells.

Description (Figs. 52–56, 78–89): Similar to that of *E. chrysippe*, except as described below. Approximately 0.45 mm diameter; opaque yellowish pale brown to creamy-white with apical rim area purplish-brown; edge of pigmentation beyond apical rim uneven up to ca. one-sixth of egg height (Figs. 53–54); width of crenulated rim narrow, ca. one-seventh of dorsal surface diameter; three micropyles on innermost circle; first and second rows complete (11 on first and 15 on second row), third incomplete with a few closed cells.

Material examined: Laguna de Hule, 2003 (n = 3 live egg masses; SEM, n = 2 eggs).

TABLE 5. Number, location, and type of setae on pupa of *Euselasia chrysippe* and *E. bettina*. (numbers on one side); CBS = clubbed seta; * = including setae in frontal area, and short slender setae were not counted here.

	E. chrysippe (n = 4)			*E. bettina* (n = 4)		
Segment	CBS on dorsum	CBS on subdorsum to lateral	long slender seta on lateral to subventer	CBS on dorsum	CBS on subdorsum to lateral	long slender seta on lateral to subventer
T1	1	9*	8–10*	1	8–10*	8–9*
T2	5	1	0	5	1	0
T3	2	1	0–2	1–2	1	2
A1	1	0	0	1	0	0
A2	2	3	2	2	3–4	1–2
A3	2	3	2	2	3	2
A4	2	2–3	2–4	2	2	3
A5	2	1	1–3	2	1	2–5
A6	2	1	2–3	2	1	1–4
A7	2	2	0–2	2	2	2–3
A8+9	1	0	1–2	1	0	1–2
A10	0	0	3 (on dorsum to subdorsum)	0	0	3 (on dorsum to subdorsum)

FIRST INSTAR LARVA

Diagnosis: The head capsule width of *Euselasia bettina* is ca. 0.25 mm; the head is semi-translucent pale-brown; the body color is slightly darker and less translucent than *E. chrysippe*; and the proleg on A10 has 8–9 crochets in lateroseries. In *E. chrysippe* the head capsule width is narrower (ca. 0.20 mm) and translucent pale-brown; the body color is more translucent; and the proleg on A10 has less crochets (7).

Description (Figs. 57–59, 90–135): Similar to *E. chrysippe*, except as described below. Body length 0.8–2.2 mm. Head: Width ca. 0.25 mm, semi-translucent pale-brown, slightly darker than *E. chrysippe*; proleg on A10 with 8–9 uniordinal crochets in lateroseries in semicircle and 4–5 uniordinal crochets in mesoseries.

Material examined: Laguna de Hule, 2003 (SEM, n = 3; dissecting stereo-microscope, n = 1).

SECOND INSTAR

Diagnosis: The head capsule width of *Euselasia bettina* is ca. 0.35 mm; the body is gray with dark-gray to black dorsal pinacula; the proleg on A10 has 11–12 uni- to biordinal crochets in lateroseries and six uniordinal crochets in mesoseries. In *E. chrysippe* the head capsule width is narrower (ca. 0.33 mm); the body is pale grayish-green without dark dorsal pinacula; and the proleg on A10 has less crochets (9–10 uniordinal crochets in lateroseries and five crochets in mesoseries).

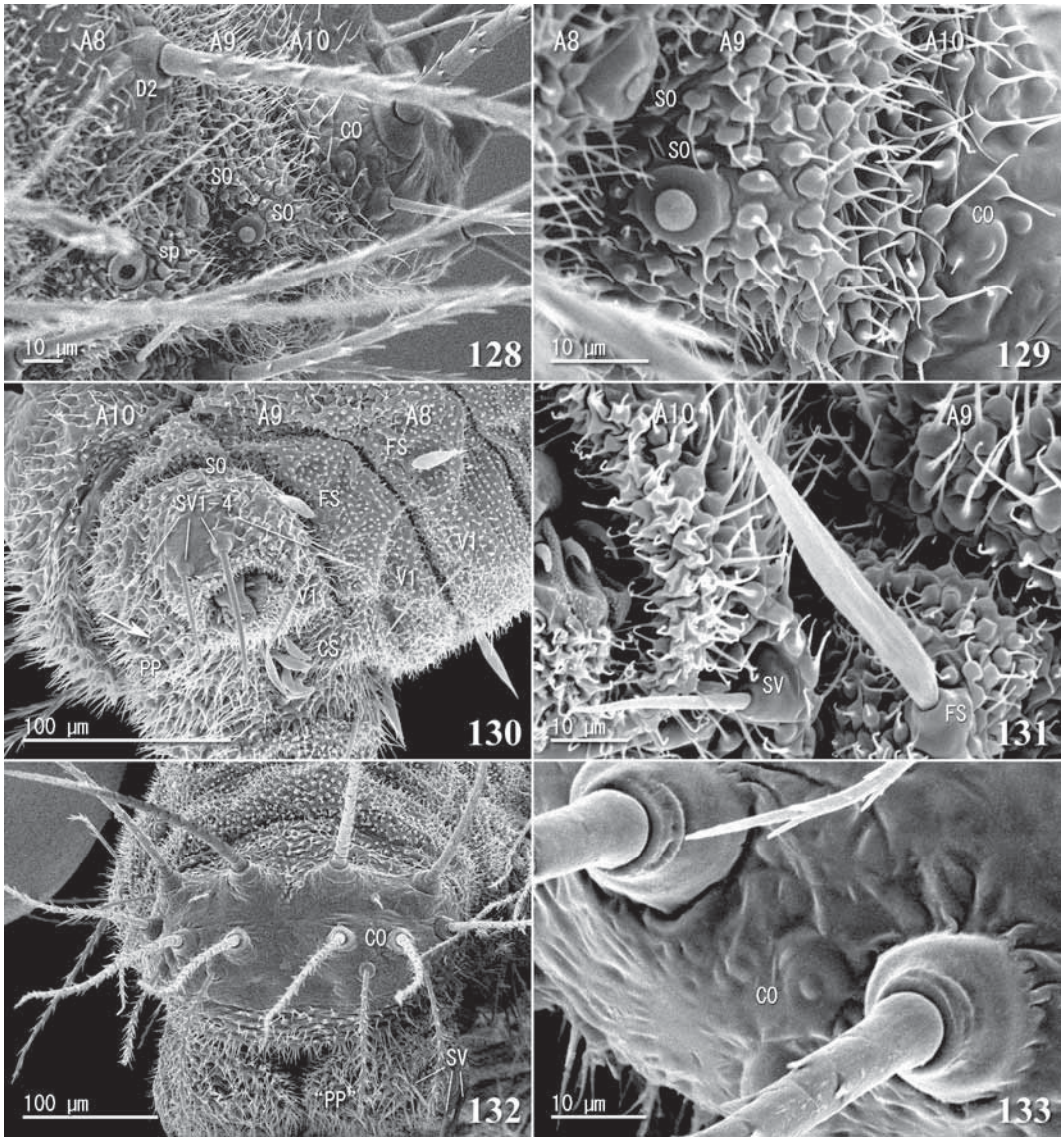
Description (Fig. 61): Similar to *E. chrysippe*, except as described below. Body length 2.1–3.8 mm, pale-gray with dark-gray to black pinacula dorsally, mesal line and intersegmental membrane on dorsum dark-green, semi-translucent pale-brown laterally. Head: Width ca. 0.35 mm, pale orange-brown. T1: Shield pale-orange with a pair of thin, brown to dark-brown transverse lines in posterior portion. T2–3: With a pair of dark-brown to black pinacula. A1–8: With a pair of black pinacula on dorsum on each segment as in T2–3, but

pinacula wider; proleg with 6–8 uniordinal crochets in each row. A10: Anal plate with a pair of pale-brown to dark-brown transverse lines; proleg with 11–12 uni- to biordinal crochets in semicircular lateroseries and six uniordinal crochets in mesoseries.

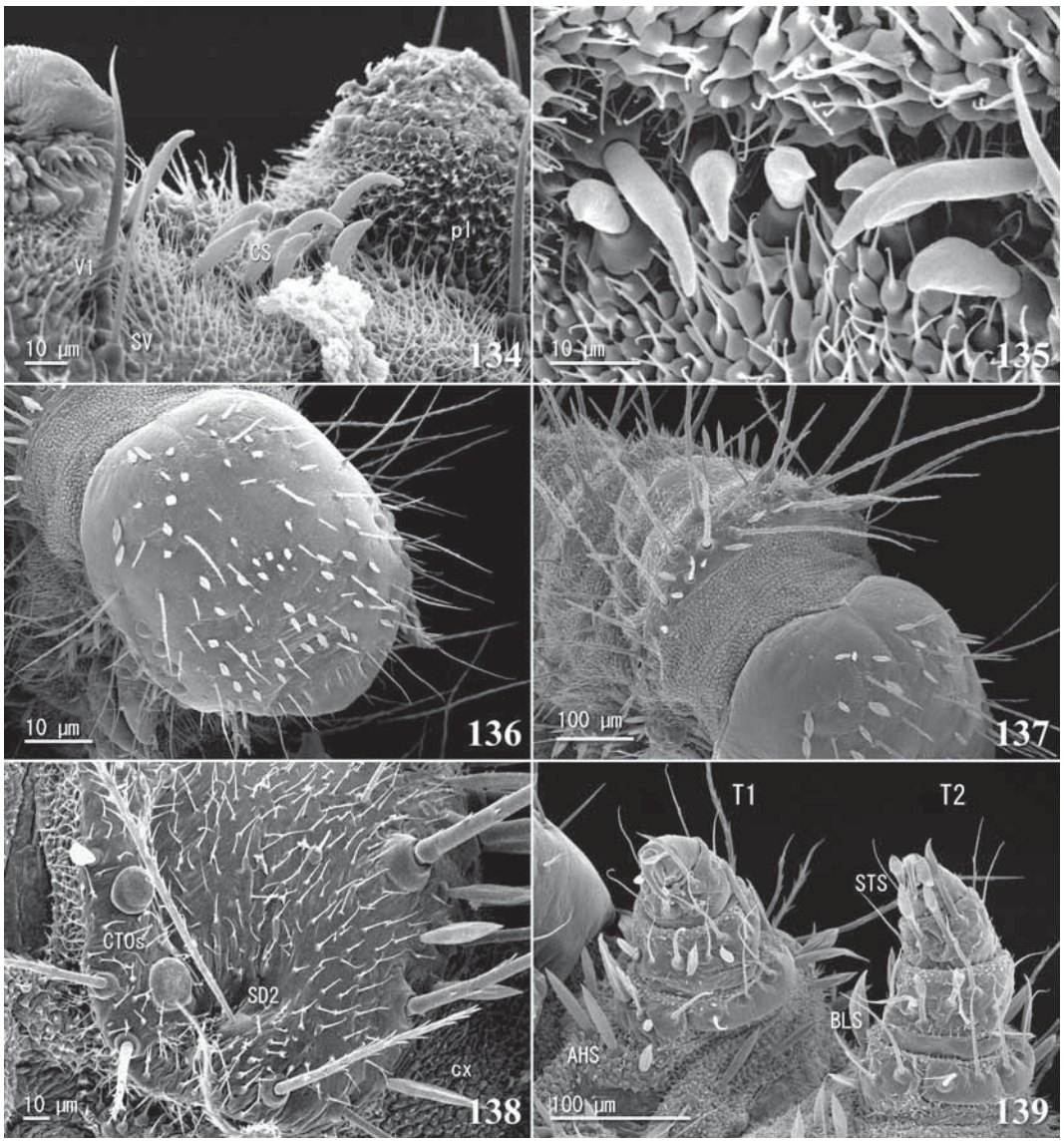
Material examined: Laguna de Hule, 2003 (dissecting stereo-microscope, n = 1).

THIRD INSTAR

Diagnosis: The head capsule width of *Euselasia bettina* is ca. 0.55 mm; the body is gray with a pair of transverse black lines on T1 shield and prominent black pinacula on dorsum of T2–A8; the dorsal mesal line, intersegmental membrane, and anal plate are black; and the proleg on A10 has 8–9 uniordinal crochets in mesoseries. In *E. chrysippe* the head capsule is slightly narrower (ca. 0.53 mm); the body is greenish-pale-gray; the T1 shield is pale-orange; the dorsum of T2–A8 has a pair of gray pinacula, becoming faint posteriorly; the dorsal mesal line and intersegmental membrane are dull green; anal plate is pale-gray; and the proleg on A10 has slightly less crochets (6–7) in mesoseries.



FIGURES 128–133. SEM of *Euselasia* first instar. **128)** Spherical organs (SO) and cupola organ (CO) on A8–10, lateral view (*E. chrysippe*); **129)** Spherical organs (SO) and cupola organ (CO) on left side of A8–10, lateral view (*E. chrysippe*); **130)** Flat seta (FS), SV- and V-group, spherical organ (SO), and claw-shaped setae (CS) on A8–10, ventro-lateral view (*E. chrysippe*); **131)** Flat seta (FS) on right side of A9 (*E. chrysippe*); **132)** A9–10 and arrangement of setae on anal plate, caudal view (*E. chrysippe*); **133)** Cupola organ (CO) in D2 triangular setal group on A10, caudo-lateral view (*E. bettina*).

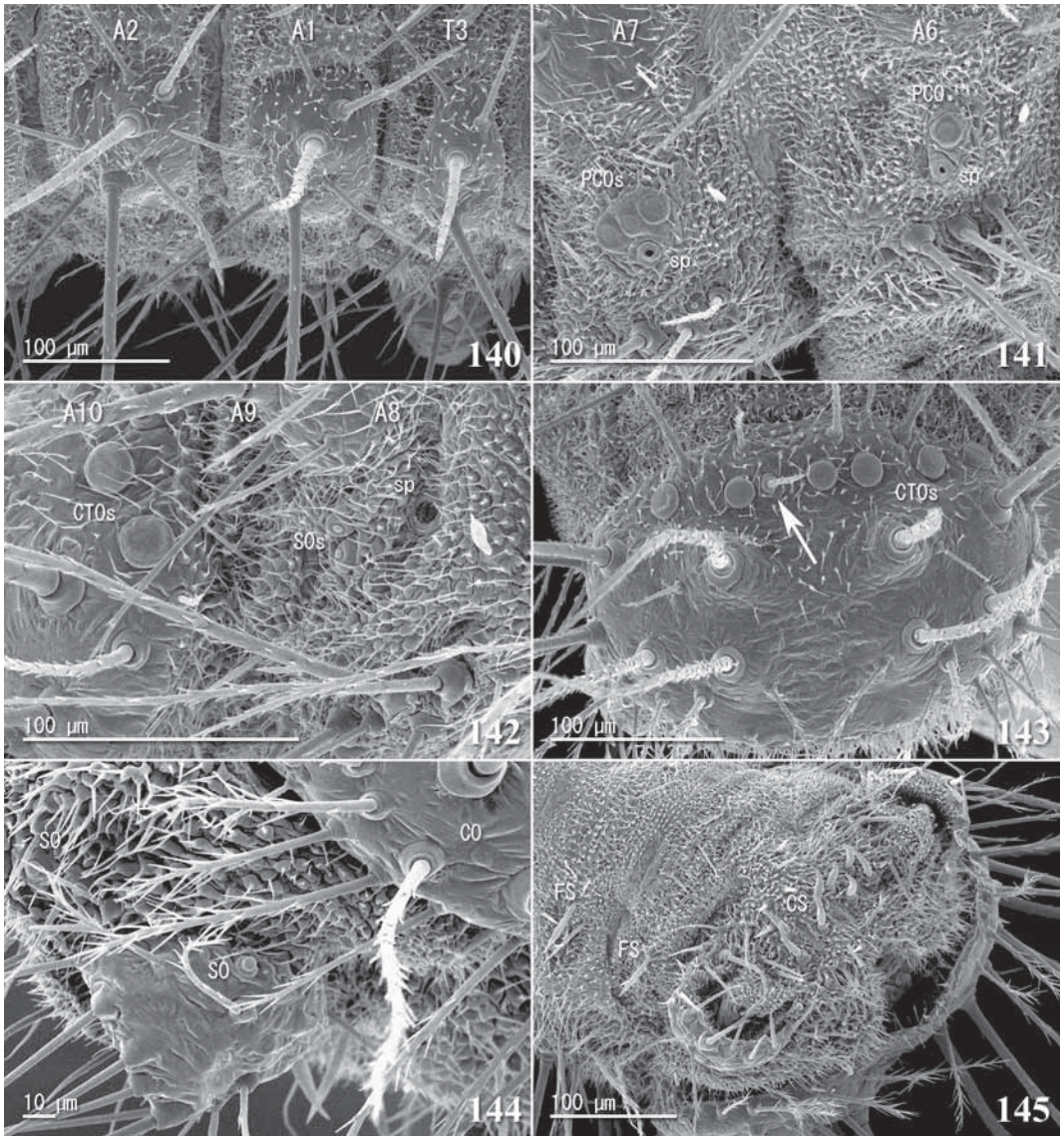


FIGURES 134–135. SEM of *Euselasia* first instar and **FIGURES 136–139.** SEM of *E. chrysippe* second instar. **134)** Claw-shaped setae (CS) area between prolegs on A10, ventral view (*E. bettina*); **135)** Claw-shaped setae ventral view (*E. chrysippe*); **136)** Head, frontal view; **137)** Head and T1–2, fronto-dorsal view; **138)** T1 shield showing setae and circular tablet organs (CTOs), lateral view; **139)** T1–2 legs showing arrowhead setae (AHS), bladelike seta (BLS), and spatulate-tipped setae (STS), ventro-lateral view.

Description (Figs. 62–63, 148): Similar to previous instar and *E. chrysippe* except as described below. Body length 3.7–5.2 mm, with black and orange color more prominent; spherical organs sparsely scattered over body surface (as in other instars). **Head**: Width 0.55 mm, dull orange, with more setae and arrowhead setae than previous instar. **Thorax and abdomen.** T1: Shield pale-orange in anterior half with eight pairs of setae projecting dorso-anteriorly; posterior half with a pair of black transverse lines; three pairs of circular tablet organs and 3–4 pairs of setae near latero-posterior margin; bladelike seta somewhat arrowhead-shaped; spatulate-tipped setae (Tables 3–4). T2–A8: Pinaculum on dorsum with two brown thick, long setae and >5 semi-translucent white to pale-brown slender, short setae; more spiracular PCOs than previous instar (Table 3); proleg with 9–10 biordinal crochets on each row. A10: Anal plate with four pairs of thick brown setae and several semi-translucent white to pale-brown thinner setae projecting dorso-posteriorly and several semi-translucent white to pale-brown featherlike slender setae on lateral to posterior margins; black lines of plate

connected to each other and arch-shaped; posterior middle portion of plate whitish; twelve claw-shaped setae between prolegs (Table 3); proleg with 14 biordinal crochets in lateroseries and 8–9 biordinal crochets in mesoseries.

Material examined: Laguna de Hule, 2003 (SEM, n = 2; dissecting stereo-microscope, n = 2).



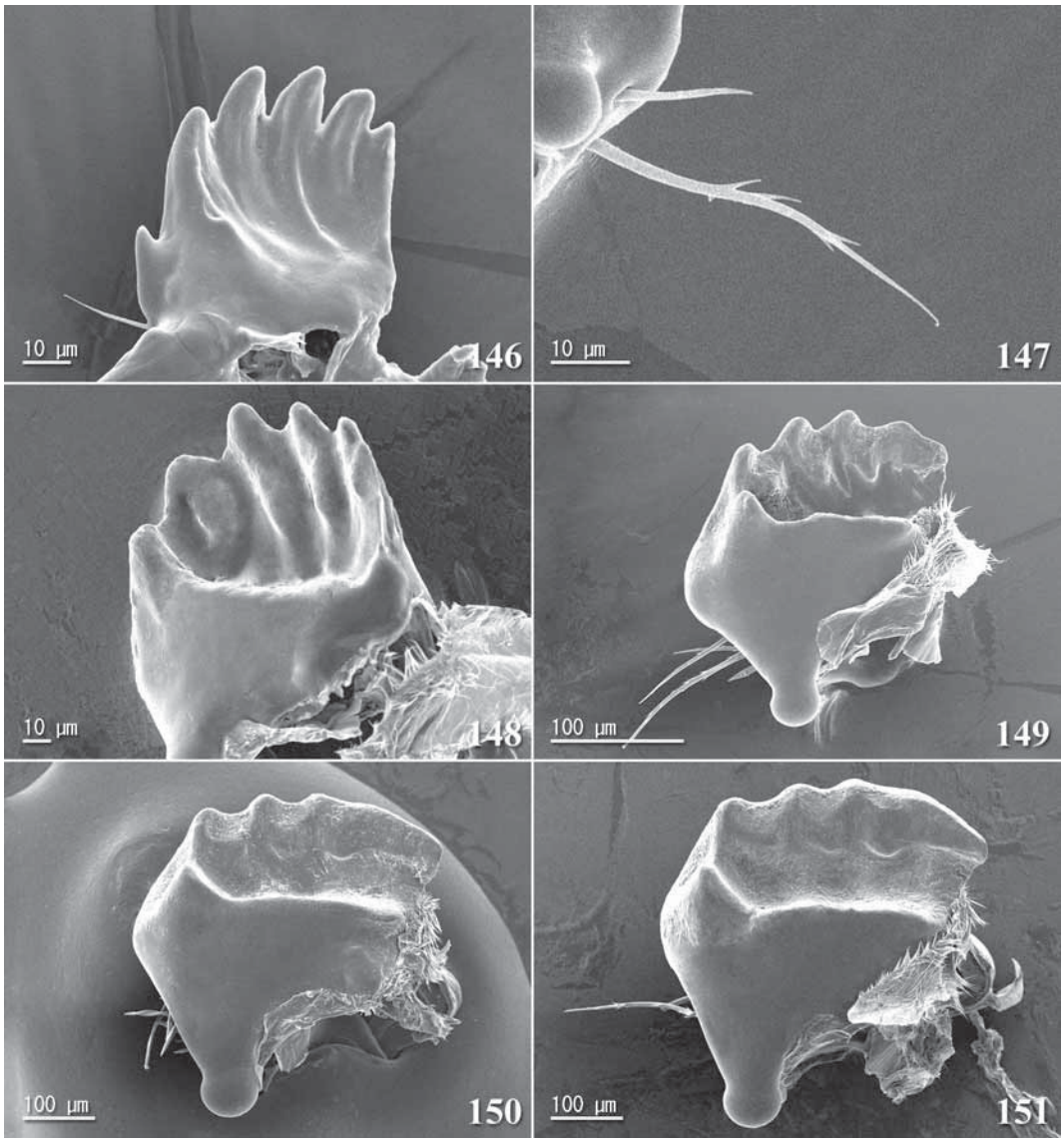
FIGURES 140–145. SEM of *E. chrysippe* second instar. **140)** Arrangement of D-group on T3–A2, dorsal view; **141)** PCOs contiguous to spiracles on A6–7, lateral view; **142)** spherical organs (SO) and circular tablet organs (CTOs) on right side of A8+9–A10, lateral view; **143)** Anal plate showing setal arrangement and circular tablet organs (CTOs) (circular tablet organ replaced with a seta = arrow, and left end circular tablet organ missing), dorso-caudal view; **144)** Cupola organ (CO) on anal plate and spherical organs (SO) on proleg on right side A10, dorso-lateral view; **145)** Flat seta (FS) on A8–9 and claw-shaped setae (CS) between A10 prolegs, ventral view.

FOURTH INSTAR

Diagnosis: The head capsule width of *Euselasia bettina* is ca. 0.80 mm; the overall body color is grayish-yellow; the T1 shield is mostly black; the pinacula on dorsum are prominently blackl the mesal line and intersegmental membrane are dark-green; the proleg on A10 has 25–26 biordinal crochets in lateroseries. In *E. chrysippe* the head capsule width is slightly narrower (ca. 0.72 mm); the overall body color is grayish-green; the T1 shield is mostly orange; the pinacula on dorsum are dull black; the mesal line and intersegmental membrane are dull green; and the proleg on A10 has 20–22 crochets in lateroseries.

Description (Figs. 63–65): Similar to of *E. chrysippe* and previous instar, except as described below. Body length 7.6–9.8 mm, recently molted larvae dark-gray with prominent black pinacula (Fig. 63), mid- to late-stage larvae grayish-yellow. Mesal line and intersegmental membrane dark-green. **Head**: Width 0.80 mm, dark-brown to black. **Thorax and abdomen.** T1: Shield dark-brown to black, slightly orange to yellowish frontally. T2–8: With black pinaculum on dorsum; a faint white longitudinal line subdorsally along lateral lobes; proleg with 14–17 biordinal crochets in each row. A10: Posterior middle portion of anal plate prominently white; proleg with 25–26 biordinal crochets in lateroseries and 12–13 biordinal crochets in mesoseries.

Material examined: Laguna de Hule, 2003 (dissecting stereo-microscope, n = 3).



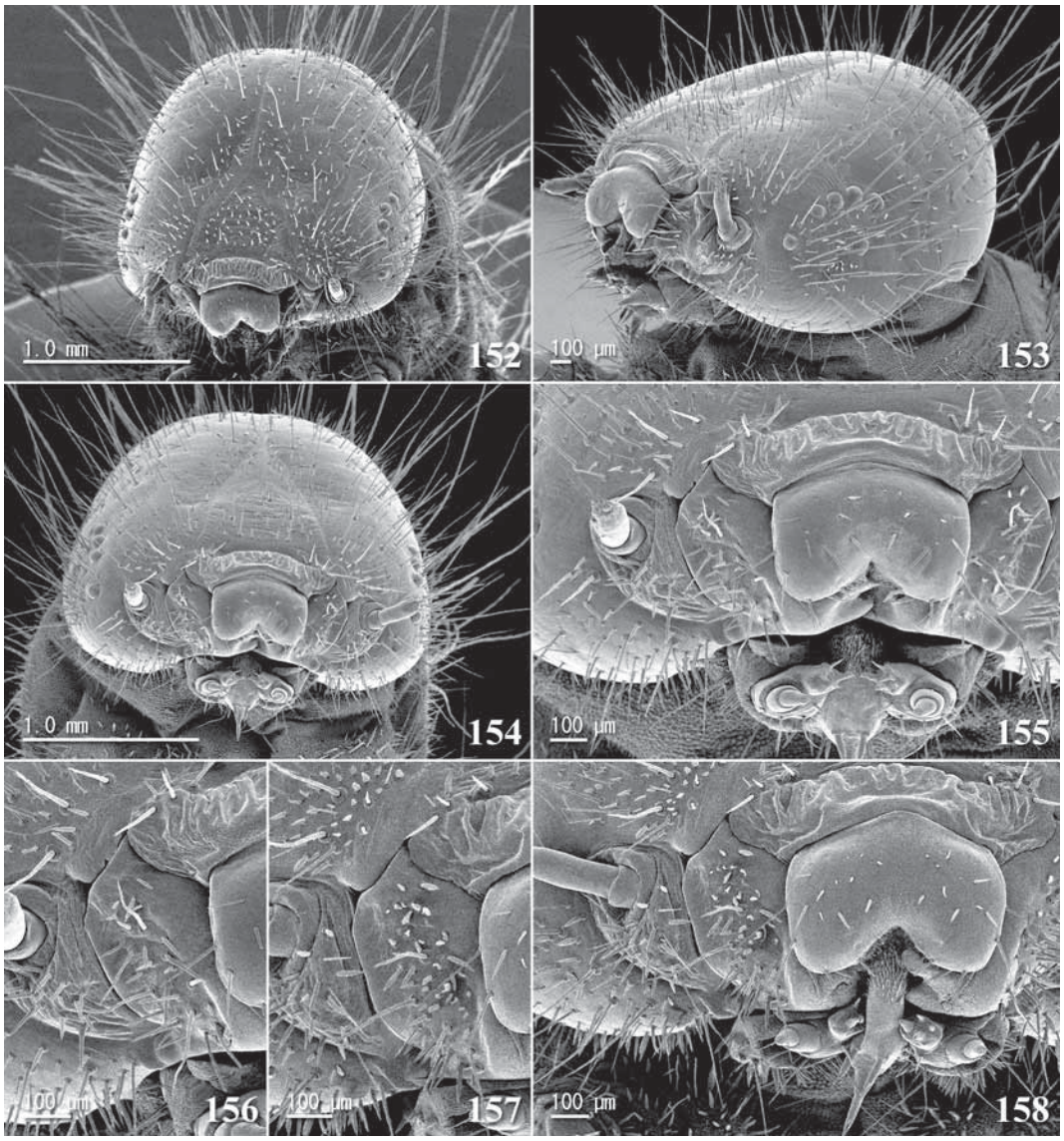
FIGURES 146–151. SEM of mandibles of *Euselasia* (inner surface). **146)** First instar, left (*E. chrysippe*); **147)** First instar right mandibular setae, inner view (*E. chrysippe*); **148)** Third instar, left (*E. bettina*); **149)** Fourth instar, left (*E. chrysippe*); **150)** Sixth instar, left (*E. chrysippe*); **151)** Sixth instar, left (*E. bettina*).

FIFTH INSTAR

Diagnosis: The fifth instar of *Euselasia bettina* is greenish-black to greenish-dull yellow with prominent black pinacula on dorsum; the head capsule is ca. 1.30 mm wide; the T1 shield is entirely or mostly black with a little orange; and the proleg on A10 has 15–16 crochets in a mesoseries. The fifth instar of *E. chrysippe* is gray to yellowish-gray with less promiment black pinacula; the head capsule is slightly narrower (ca. 1.23 mm); the T1 shield is mostly orange; and the proleg on A10 has 11–13 crochets in mesoseries.

Description: (Figs. 66–68). Similar to *E. chrysippe* and previous instar, except as described below. Body length 10.0–14.5 mm; overall color slightly darker and with larger and prominent black pinacula on dorsum compared to *E. chrysippe* fifth instar (Fig. 68); recently molted and early stage dark as in fourth instar, but slightly greenish (Fig. 66) and with whitish-pale color around black pinacula on dorsum; overall color becoming paler as larva matures (Figs. 67–68). **Head**: Width 1.30 mm, black. **Thorax and abdomen.** T1: Shield dark-brown to black or dark-brown with pale-yellow to orange. A3–6: Proleg with 21–24 biordinal crochets on each row. A10: Proleg with 32–36 biordinal crochets in lateroseries and 15–16 biordinal crochets in mesoseries.

Material examined: Laguna de Hule, 2003 (dissecting stereo-microscope, n = 3)

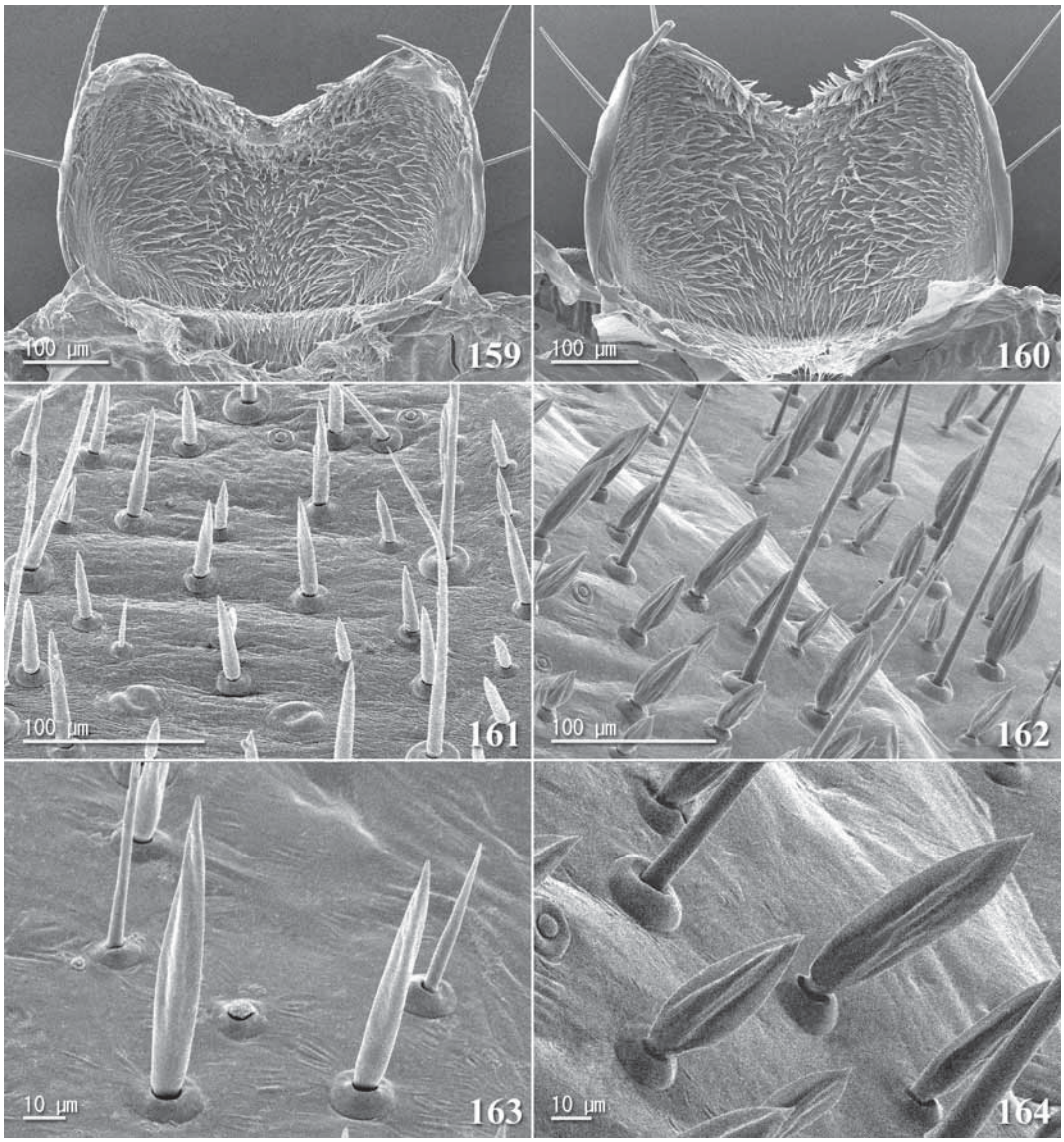


FIGURES 152–158. SEM of *Euselasia* sixth instar. **152)** Head, frontal view (*E. chrysippe*); **153)** Head, latero-frontal view (*E. chrysippe*); **154)** Head, frontal-ventral view (*E. chrysippe*); **155)** Mouthparts, frontal view (*E. chrysippe*); **156)** Areas between labrum and antenna, frontal view (*E. chrysippe*); **157)** Areas between labrum and antenna, frontal view (*E. bettina*); **158)** Mouthparts, frontal view (*E. bettina*).

SIXTH INSTAR

Diagnosis: The sixth instar of *Euselasia bettina* is brownish-amber with reddish or greenish tint; the head capsule is ca. 1.75 mm wide; the color of the head is black with a pair of brownish-orange to pale-orange patches running parallel to the epicranial suture; the arrowhead setae are flattened as in the first instar; the

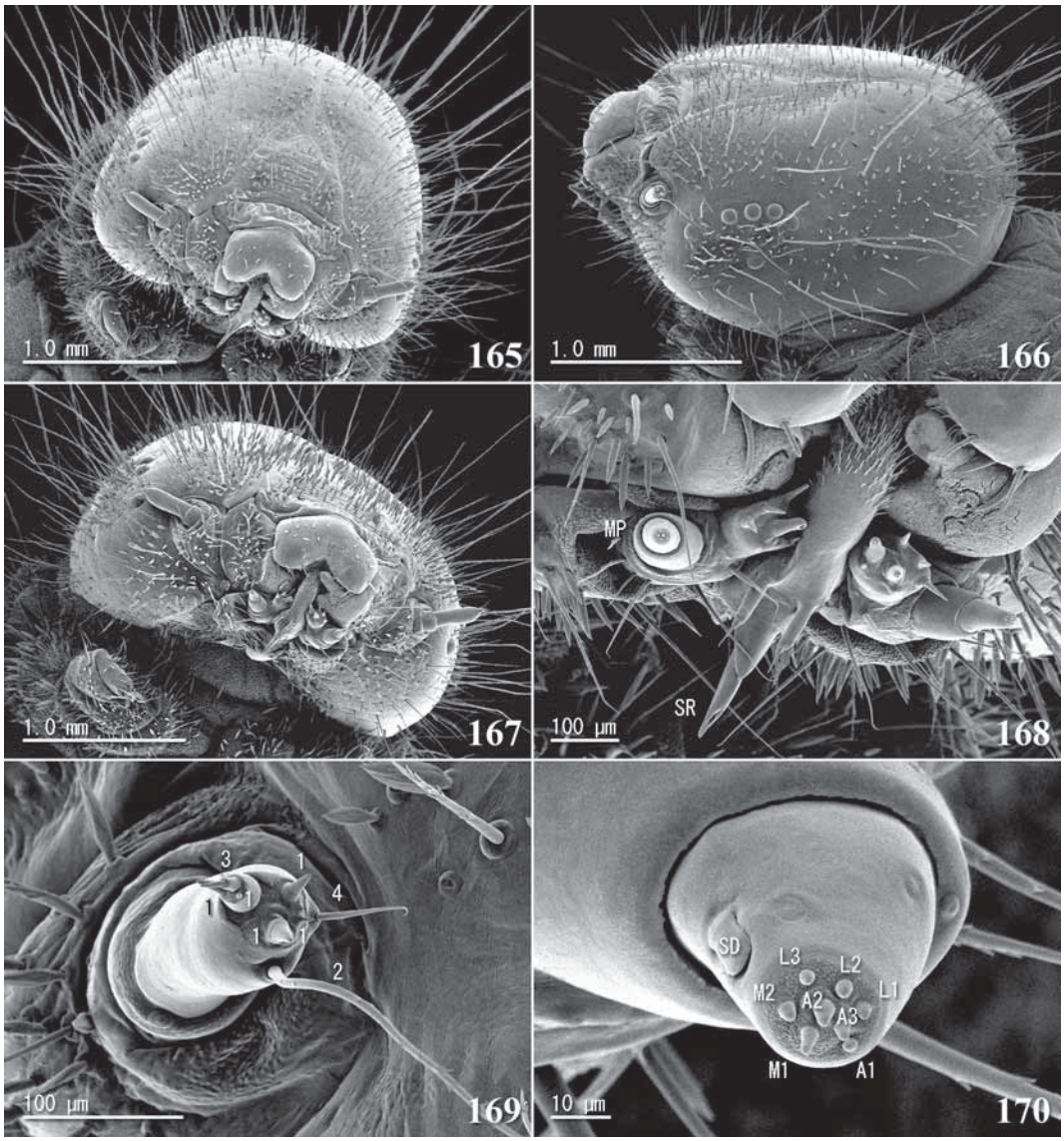
curvature of ventral margin of labrum is widely angled (ca. 120°); the mandible is large (ca. 0.45 mm wide) with more distinct dentition than in *E. chrysippe*; the T1 shield is bright orange with reddish tint, with black transverse lines with a faint bluish-gray iridescence; the pinacula on the dorsum is black with an oval white line; the iridescence of the structural color plates is bright and metallic sky-blue; and the proleg on A10 has biordinal 15–16 crochets in mesoseries. The sixth instart of *E. chrysippe* is greenish-dark-gray to greenish-dull black; the head is slightly narrower (ca. 1.65 mm) and bright orange or black, or intermixture of these two colors; the arrowhead setae are cone-shaped (not flattened), ridged and spiraled apically; the curvature of the ventral margin of the labrum is more narrowly angled (ca. 110°); the mandible is smaller (0.38 mm wide) with less distinct dentation; the T1 shield is orange to bright orange, without iridescence; the oval line on the dorsal pinacula is pale-gray; the iridescence of the structural color plate is less bright, faint metallic-blue; and the proleg on A10 has 11–13 crochets in mesoseries.



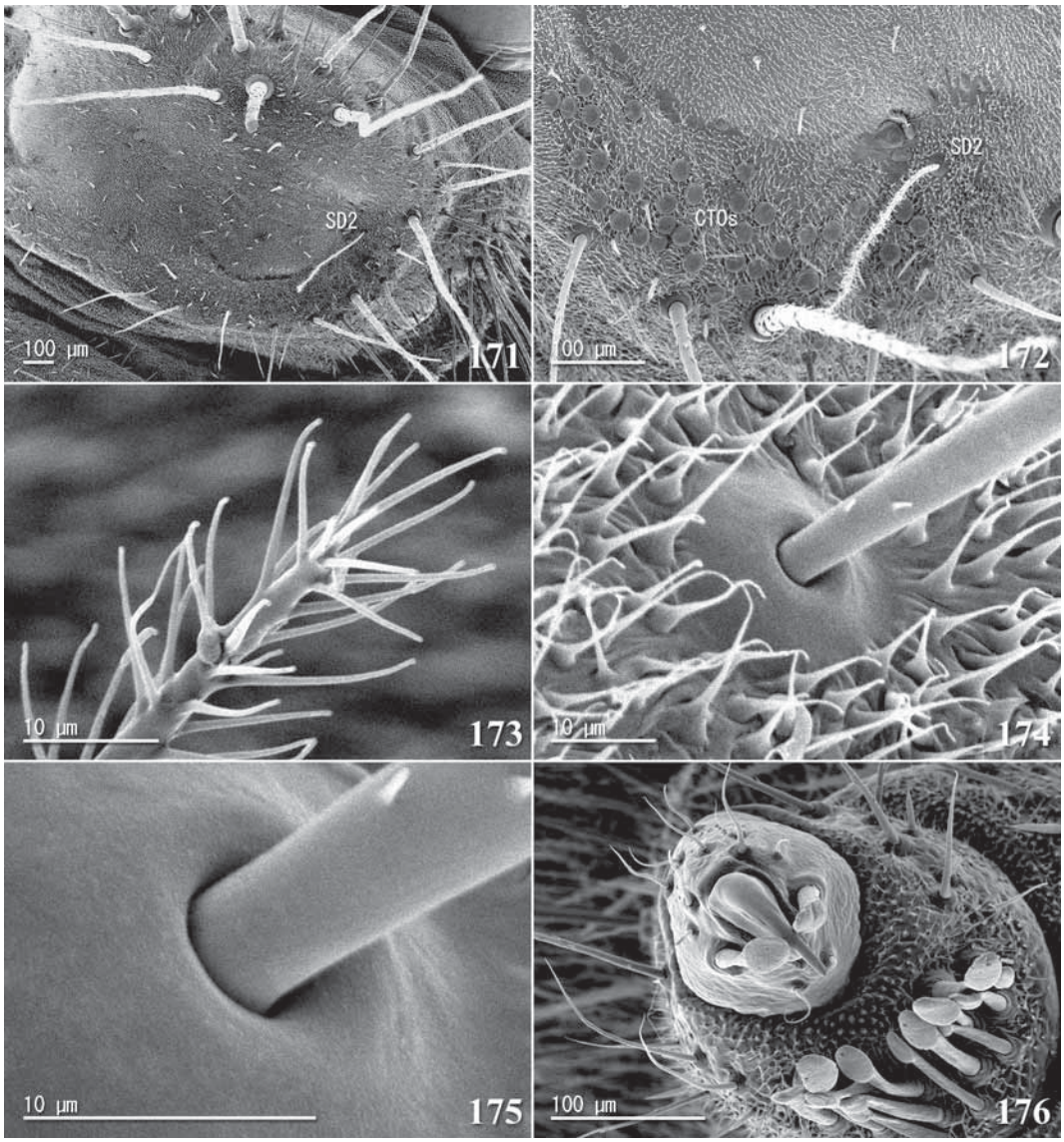
FIGURES 159–164. SEM of *Euselasia* sixth instar. **159)** Labrum, inner surface (*E. chrysippe*); **160)** Labrum, inner surface (*E. bettina*); **161)** Frons showing arrowhead setae, cupola organs, and other setae, fronto-ventral view (*E. chrysippe*); **162)** Left side frons showing adfrontal suture area and arrowhead setae, cupola organ, and other setae, fronto-lateral view; **163)** Arrowhead setae of figure 161 (*E. chrysippe*); **164)** Arrowhead setae of figure 162 (*E. bettina*).

Description: (Figs. 68–73, 157–158, 160, 162, 164–207). Similar to *E. chrysippe* and previous instar except as described below. Body length 15.0–22.0 mm, coloration most distinct from all other instars and *E. chrysippe*; brownish-amber with reddish or greenish tint, mesal line on dorsum and intersegmental membrane dull black to dark-green. **Head** (Figs. 70, 72–73, 157–158, 160, 162, 164, 165–170): Width ca. 1.75 mm, black with a pair of brownish-orange to pale-orange patches running parallel to epicranial suture; arrowhead setae (Figs. 72, 157–158, 162, 164) flat, variable in size; labrum as figured (Figs. 158, 160), curvature of ventral margin narrowly angled (ca. 110°); mandible (Fig. 151) similar to *E. chrysippe* but larger (ca. 0.45 mm wide), dentation slightly more distinct (n = 5). **Thorax and abdomen.** T1: Shield reddish-orange to orange with black and inner portion black with faint bluish-gray iridescence. T2–A8: Pinacula on dorsum peneliptical black ring surrounding an oval white line dorsally and structural color plate subdorso-anteriorly; structural color plate with metallic sky-blue iridescence with center concave and black (Figs. 69–71, 195); proleg with 21–26 biordinal crochets on each row. A10: Anal plate with metallic sky-blue iridescence as in other segments; proleg with 31–33 biordinal crochets in lateroseries in semicircle and 15–16 biordinal crochets in mesoseries.

Material examined: Laguna de Hule, 2003 (SEM, n = 2; dissecting stereo-microscope, n = 3).



FIGURES 165–170. SEM of *Euselasia* sixth instar. **165)** Head, frontal-ventral view (*E. bettina*); **166)** Head, latero-frontal view (*E. bettina*); **167)** Head, ventral view (*E. bettina*); **168)** Oral area showing spinneret and maxillary palpus (*E. bettina*); **169)** Left antenna showing sensillar arrangement, frontal view (*E. bettina*); **170)** Left maxillary palpus showing sensillar arrangement (*E. chrysippe*).



FIGURES 171–176. SEM of *Euselasia* sixth instar (*E. chrysippe*). **171)** T1 shield, dorsal view; **172)** Right side latero-posterior margin of T1 shield showing SD2, other setae, and circular tablet organs (CTOs), dorsal view; **173)** SD2 seta near apex, lateral view; **174)** Basal area of SD2 seta, dorso-lateral view; **175)** Socketed area of SD2, dorso-lateral view; **176)** Bladelike seta on right T1 leg, ventro-lateral view.

PREPUPA

Diagnosis: The prepupa of *Euselasia bettina* is amber with black. That of *E. chrysippe* is dark brownish-gray with pale-brown.

Description (Fig. 75): Length 13.2–13.7 mm (n = 3); overall color amber with black.

Material examined: Laguna de Hule, 2003 (n = 15).

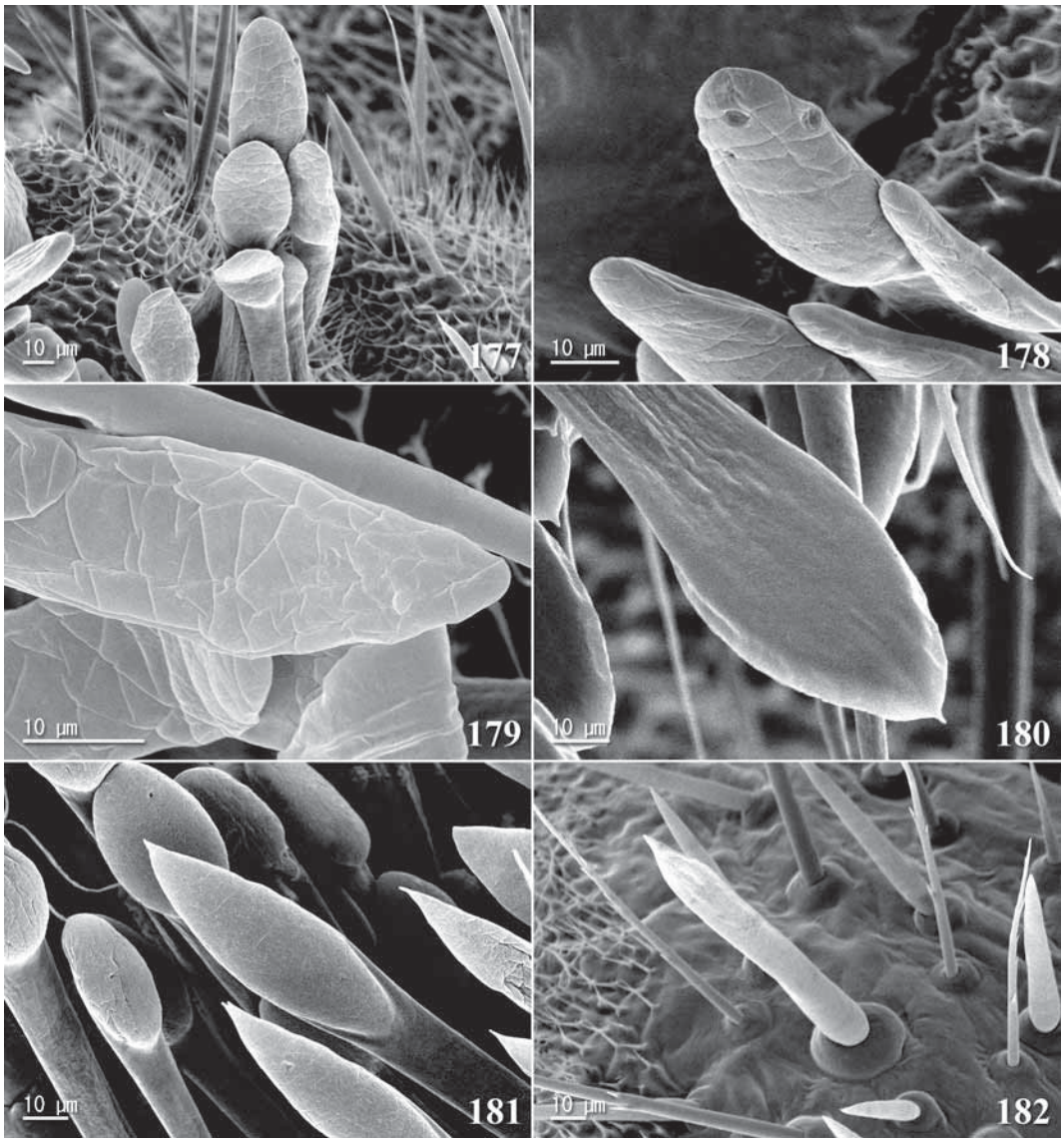
PUPA

Diagnosis: The pupa of *Euselasia bettina* is 11.4–13.5 mm long and 5.7–6.4 mm wide. That of *E. chrysippe* is usually smaller, 11.5–12.0 mm long and 5.0–5.5 mm wide.

Description (Figs. 76–77, 208–225): Similar to *E. chrysippe* except as described below. Length 11.4–13.5 mm, width 5.7–6.4 mm, depth 2.5–3.5 mm; dark-brown to black areas more prominent; pupal shell colorless semi-translucent in thorax, head, and wing sclerite, intersegmental membrane A4–5 and A5–6 orange-brown,

occasionally with brown spots on center of each eye; weak sculturing on outer one-third of eye, basal portions of antenna, prothoracic and mesothoracic legs, and proboscis, and mid- to apical area of wing sclerites; mouth parts as figured (Figs. 210–211), most specimens examined (8 of 10) with widened clypeus and broadened mandibles as in Fig. 210; some specimens more like Fig. 211 with narrower clypeus and mandibles, i.e., frons and clypeus-mandible area forming straight parallel lines; middle portion of eye with a notch at posterior end; notch absent in some specimens.

Material examined: Laguna de Hule, 2003 (SEM, n = 2 complete specimens and 2 shells; dissecting stereo-microscope, n = 3 complete specimens and 10 shells).



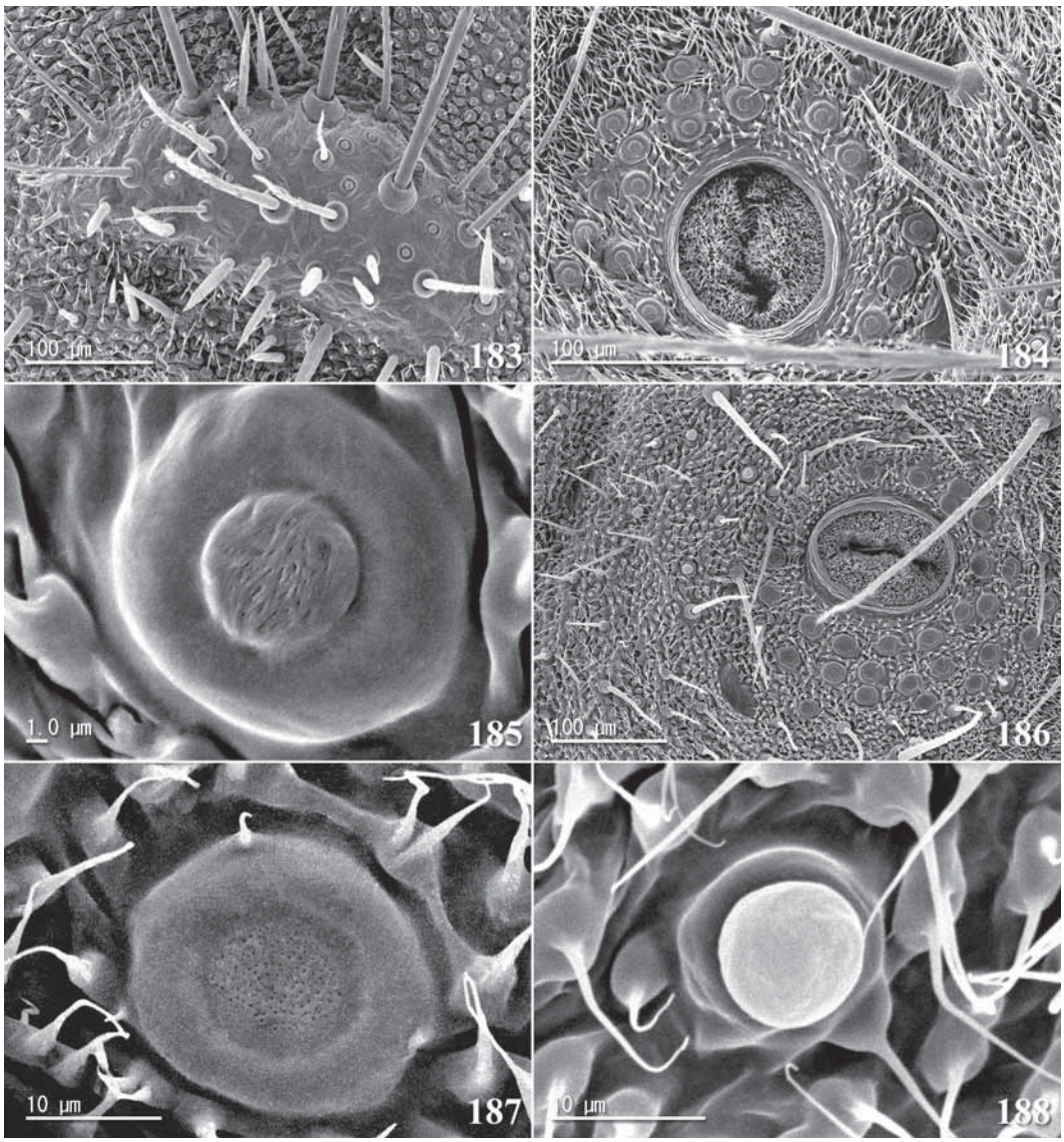
FIGURES 177–182. SEM of *Euselasia* sixth instar. **177)** Spatulate-tipped setae on right T2 leg, ventral view (*E. chrysippe*); **178)** Spatulate-tipped setae on tibia of right T1 leg, ventral view (*E. chrysippe*); **179)** Spatulate-tipped setae on tibia of right T1 leg, ventro-lateral view (*E. chrysippe*); **180)** Ventral surface of spatulate-tipped setae on tibia of left T2 leg (*E. chrysippe*); **181)** Dorsal surface of spatulate-tipped setae on tibia of T1 leg (*E. bettina*); **182)** Spatulate-tipped setae on tibia and femur of right T3 leg, ventral view (note spatulate-tipped setae on femur having sharply pointed apex) (*E. bettina*).

Diagnosis and description of adult of *Euselasia chrysippe*

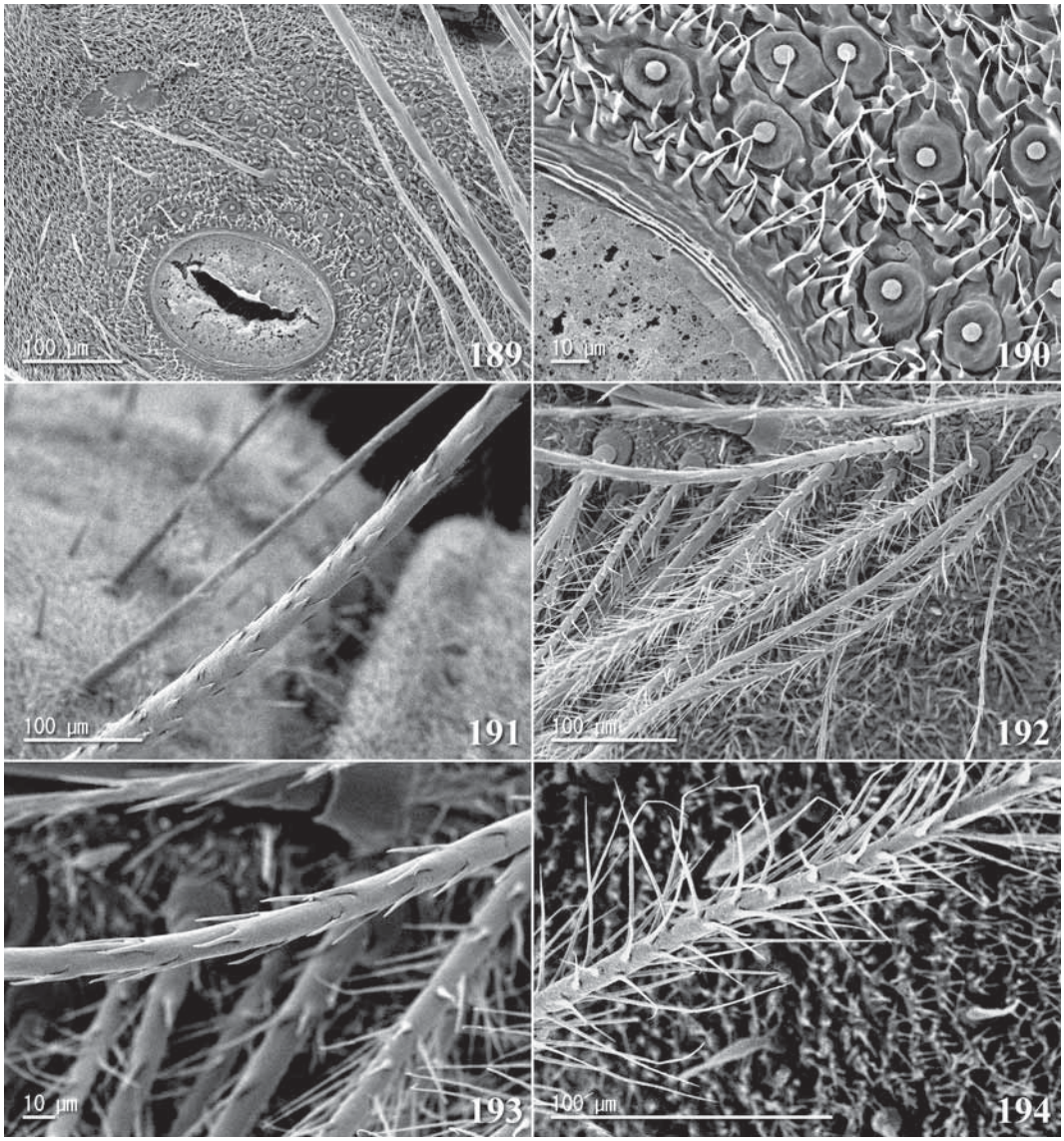
Diagnosis: The discal areas of the upper wing surface of males of *E. chrysippe* are reddish-orange; females are yellowish-orange. Both sexes have 5–7 submarginal black spots on the underside of the hindwings. The upper wing surface of both males and females of *E. bettina* are black to dark-gray. The submarginal black spots along outer margin are faint or absent, except for the apical spot.

Description: Sexually dimorphism conspicuous (Figs. 1–3, 6–7, 8, 16); six to seven small black spots (third one from apex most conspicuous) along outer submargin of hind wings in both sexes. Underside of wings more orange in male, outer margin of wings more rounded in female. For additional details of dimorphism see DeVries (1997). Rearing of a group of larvae collected in Refugio Vida Silvestre La Marta in Pejibaye de Turrialba produced several males having the upper wing surface yellowish-orange (i.e., similar to that of females) (Fig. 3).

Material examined: Lake Arenal, 2003 (n = 2 pinned males and 2 pinned females); Turrialba, 2000 (n = 22 pinned males and females).



FIGURES 183–188. SEM of *Euselasia* sixth instar. **183)** SV-group and spherical organs on right side T1, lateral view (*E. chrysippe*); **184)** Raised PCOs surrounding spiracle of left A5, lateral view (right = caudad) (*E. chrysippe*); **185)** Raised PCO of figure 184; **186)** Sunken PCOs surrounding and spherical organs near left A7 spiracle, lateral view (bottom = caudad, right = dorsal) (*E. chrysippe*); **187)** Sunken PCO (*E. bettina*); **188)** Spherical organ near A7 spiracle (*E. chrysippe*).



FIGURES 189–194. SEM of *Euselasia* sixth instar. **189)** Left A8+9 spiracle and spiracular spherical organs surrounding spiracle (top = caudad, right = ventral) (*E. chrysippe*); **190)** Spiracular spherical organs, posterior lower corner of spiracle in figure 189; **191)** dark-brown dorsal seta of left A5, lateral view (*E. chrysippe*); **192)** L-group on lateral lobe; **193)** L-group white non-plumose seta; **194)** L-group white plumose seta (*E. bettina*).

Diagnosis and description of adult of *Euselasia bettina*

Diagnosis: The upper wing surface of males and females of *E. bettina* is dark-gray to black. The submarginal black spots along the outer margin of the hindwings are inconspicuous or very faint except the one near the apex. Faint black spots are absent near the apex. Discal areas of the upperside of the wings of *E. chrysippe* are reddish-orange in the male, yellowish-orange in female, and the submarginal black spots are more conspicuous (5–7 spots).

Description: Sexual dimorphism slightly inconspicuous; male (Figs. 4, 9) with upperside of wings velvet black, female (Figs. 5, 10) dark-brown with grayish tint (DeVries 1997). Underside slightly more orange in male, outer margin of wings more rounded in female. Four to five small to faint black spots along outer submargin of hind wing of both sexes (that closest to apex larger).

Material examined: Laguna de Hule, 2003 (n = 4 pinned males and 4 pinned females).

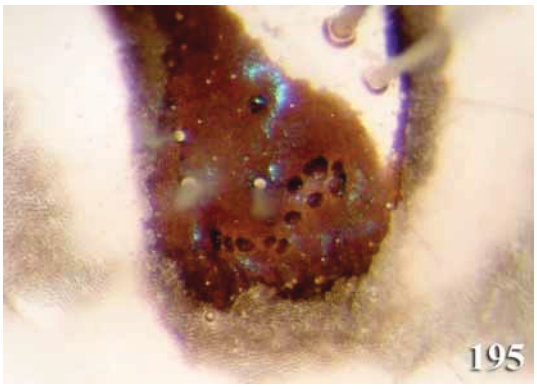
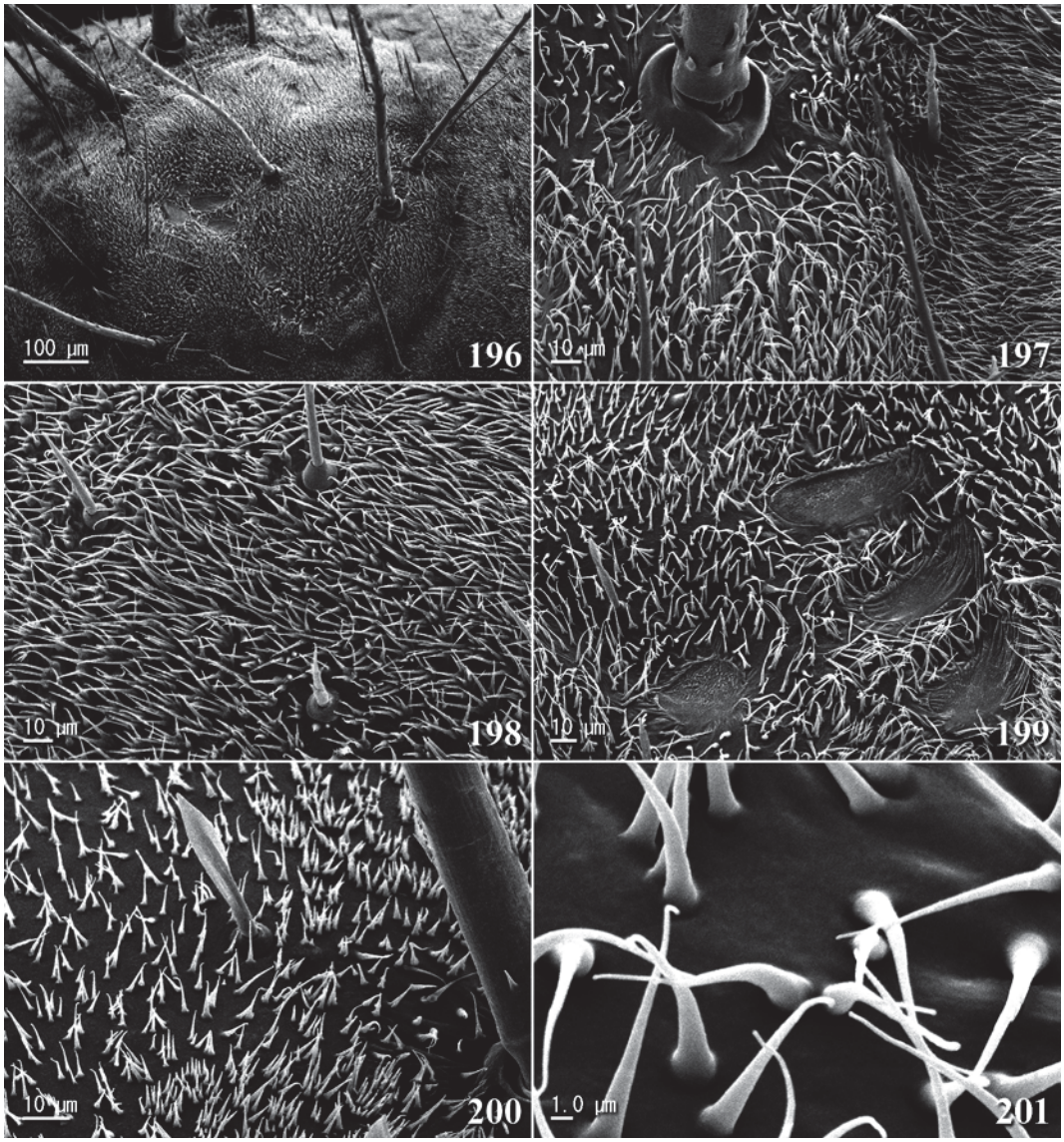
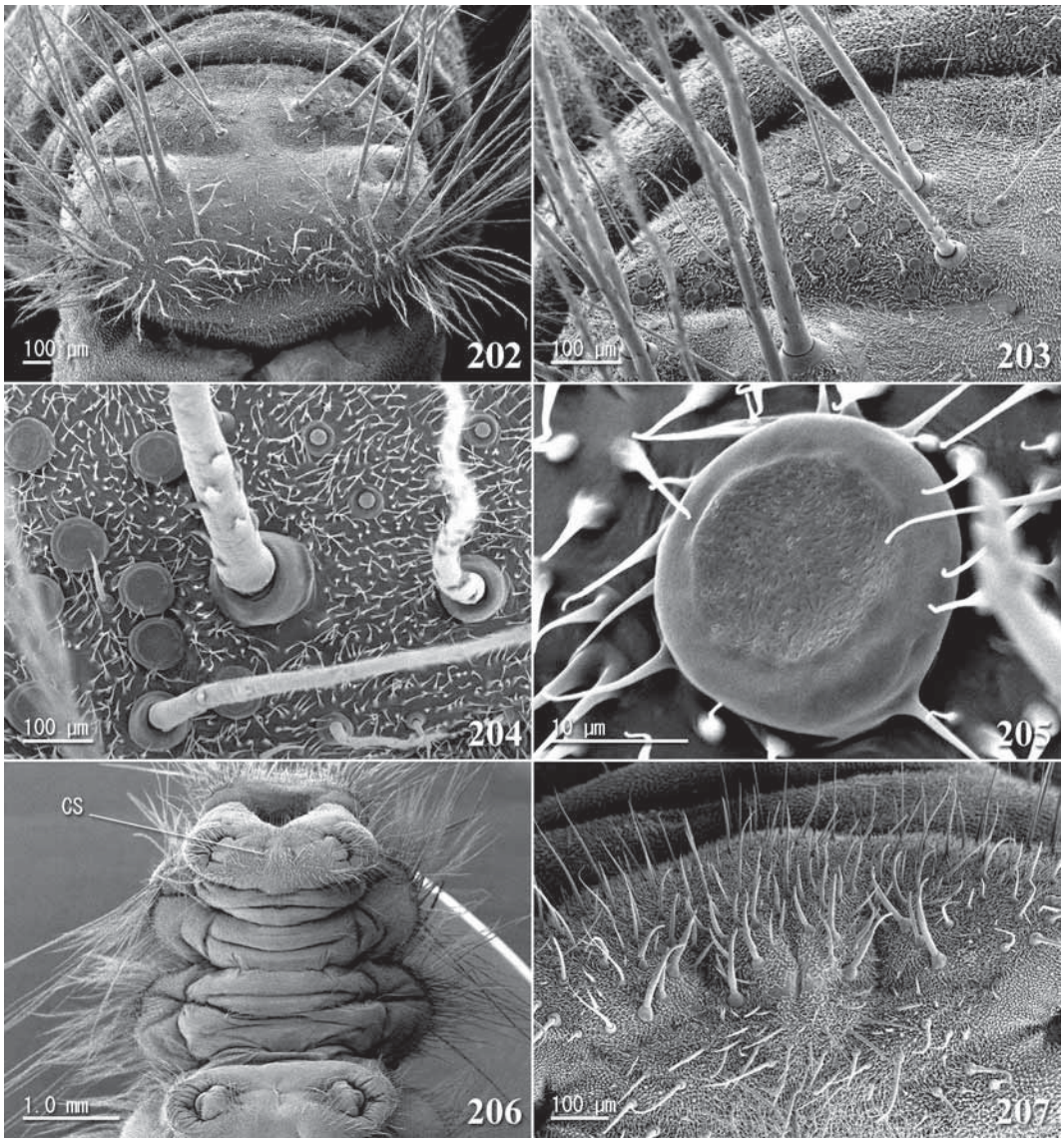


FIGURE 195. Metallic-blue iridescence of structural color plate of an EtOH preserved *E. bettina* sixth instar larva, left side A6, lateral view, left = cephalad.



FIGURES 196–201. SEM of *Euselasia* sixth instar. **196)** Pinaculum on lateral part of dorsum of abdominal segment, dorso-lateral view (right = cephalad) (*E. chrysippe*); **197)** Anterior edge of structural color plate on right A5, right side of thickly haired area = dark-pigmented area, dorso-lateral view (right = cephalad) (*E. chrysippe*); **198)** Dark-pigmented area contiguously with structural color plate (right = cephalad) (*E. bettina*); **199)** Tonofibrillary platelets in dark-pigmented area of structural color plate, dorso-lateral view (right = caudad) (*E. chrysippe*); **200)** Structural color plate, lateral view (*E. bettina*); **201)** Structural color plate surface (*E. chrysippe*).

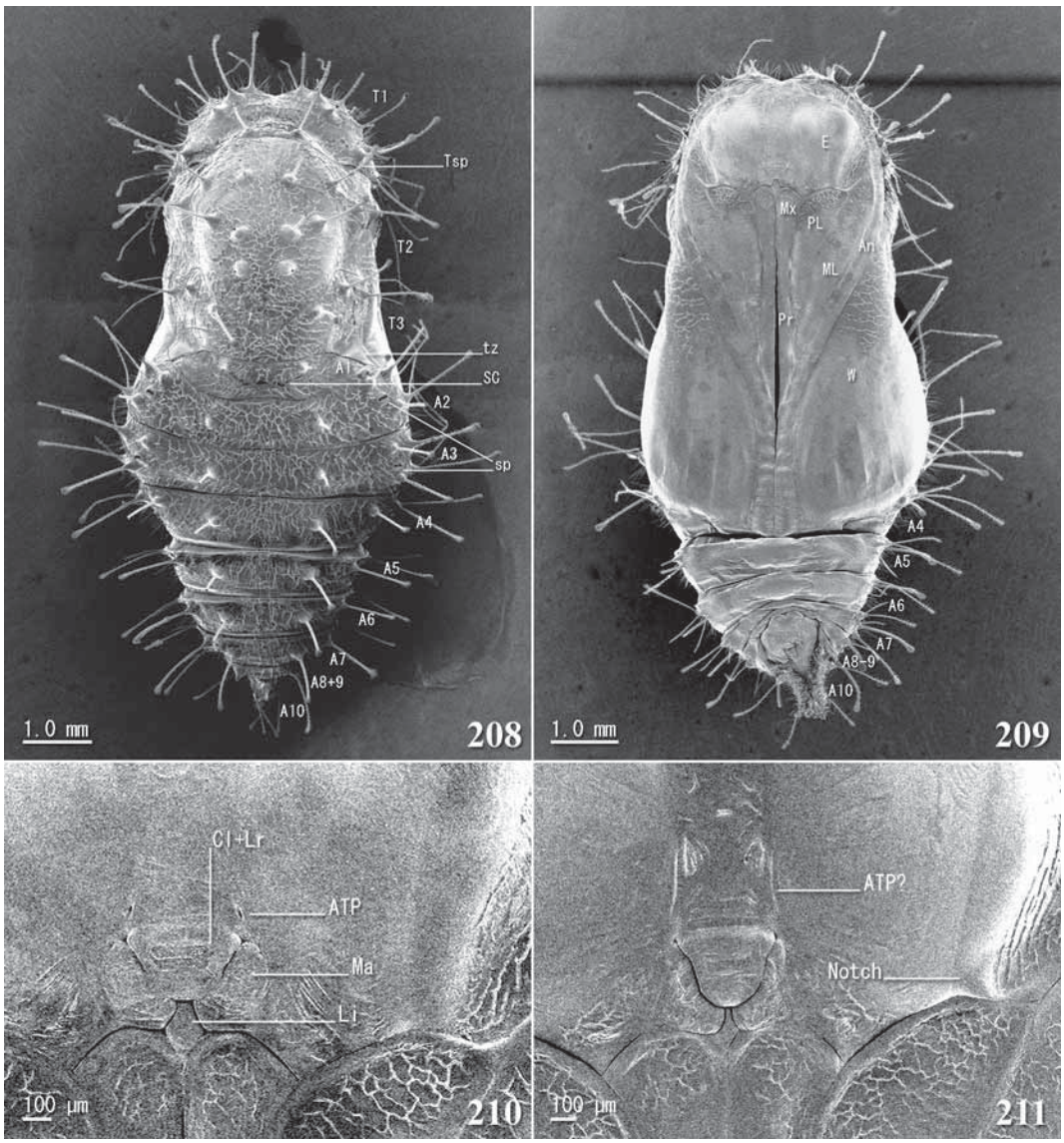


FIGURES 202–207. SEM of *Euselasia* sixth instar. **202)** Anal plate, dorso-caudal view (*E. chrysippe*); **203)** Anal plate showing circular tablet organs, dorso-caudal view (*E. chrysippe*); **204)** Anal plate showing circular tablet organs and spherical organs, dorsal view (*E. chrysippe*); **205)** Circular tablet organ on A10 (note pores on surface in linear form), dorsal view (*E. chrysippe*); **206)** Venter of A6–A10 showing L-group and claw-shaped setae (CS), ventral view (*E. bettina*); **207)** claw-shaped setae between A10 prolegs, ventral view (note more or less circular area in the center part) (*E. bettina*).

Discussion

Host plants and host specificity of *Euselasia*

Although members of *Euselasia* feed on a wide array of plant species, every species whose biology is known is stenophagous, i.e., has a very narrow host range that includes a small number of species within one to a few related genera. For example, in the field, searching for eggs and larvae on *Miconia affinis* DC. and *M. paleacea* Cogn. that were growing contiguously with *M. calvescens* did not reveal the presence of *E. chrysippe*. Also, under rearing conditions late instar larvae of *E. chrysippe* collected at Arenal did not feed on the leaves of *M. affinis* (no-choice test, n = 1 group).



FIGURES 208–211. SEM of *Euselasia* pupa. **208)** Dorsal view, (*E. chrysippe*); SC = silk clipper, sp = spiracle, Tsp = thoracic spiracle, tz = subdorsal triangular zone; **209)** Ventral view, (*E. chrysippe*); An = antenna, E = eye piece (a: inner part, b: middle, c: outer), ML = mesothoracic leg, Mx = maxilla, PL = prothoracic leg, Pr = proboscis, W = wing sclerite; **210)** Mouth parts, ventral view (*E. chrysippe*); ATP = anterior tentorial pit, Cl = clypeus, Li = labium, Lr = labrum, Ma = mandible; **211)** Mouth parts, ventral view (note notch on outer lower portion of eye piece) (*E. bettina*), ATP? = probably anterior tentorial pit.

In regards to the use of *Conostegia rufescens* as a larval host by *Euselasia chrysippe*, the genus *Conostegia* is a member of Miconieae and thus closely related to *Miconia* (Michelangeli *et al.* 2004). The preliminary results of molecular work by Michelangeli *et al.* (2004) revealed that *Miconia* is polyphyletic. The similarity of these genera is also suggested by the observation that most gall-inducing species of *Mompha* (Lepidoptera: Gelechioidea: Momphidae) in Costa Rica are found on both *Conostegia* and *Miconia* (Nishida 2005).

Although it is a preliminary assessment, *Euselasia* species can be separated into six groups on the basis of their host plant families (Table 1): a Clusiaceae group (Malpighiales), a Melastomataceae group (Myrtales), a Myrtaceae group (Myrtales), a Sapotaceae group (Ericales), a Vochysiaceae group (Myrtales), and a Euphorbiaceae group (Malpighiales) (Stevens 2009).

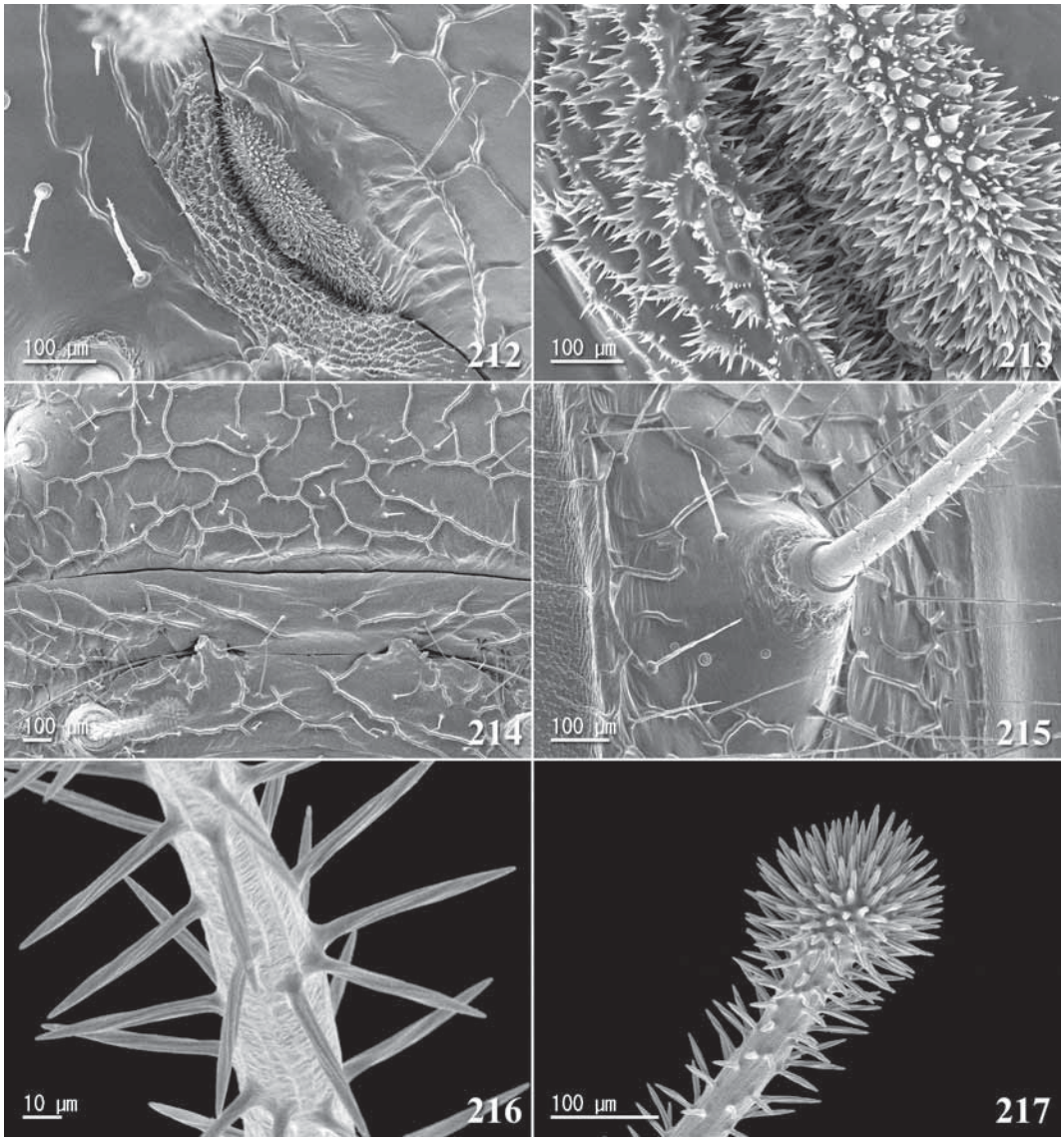
DeVries (1997) and J.P.W. Hall (pers. comm. 2006) mention that cryptic species are common in *Euselasia*. For example, the wing pattern of the adults of *Euselasia 'hygenius' DHJ01* in northwestern Costa Rica (Jan-

zen & Hallwachs 2009) and *E. hygenius* in Brazil are extremely similar, but based on the mitochondrial gene COI, the two are different species. Larvae of the former were found on Clusiaceae (Janzen & Hallwachs 2009) and those of the latter on Myrtaceae (Beccaloni *et al.* 2008, etc.).

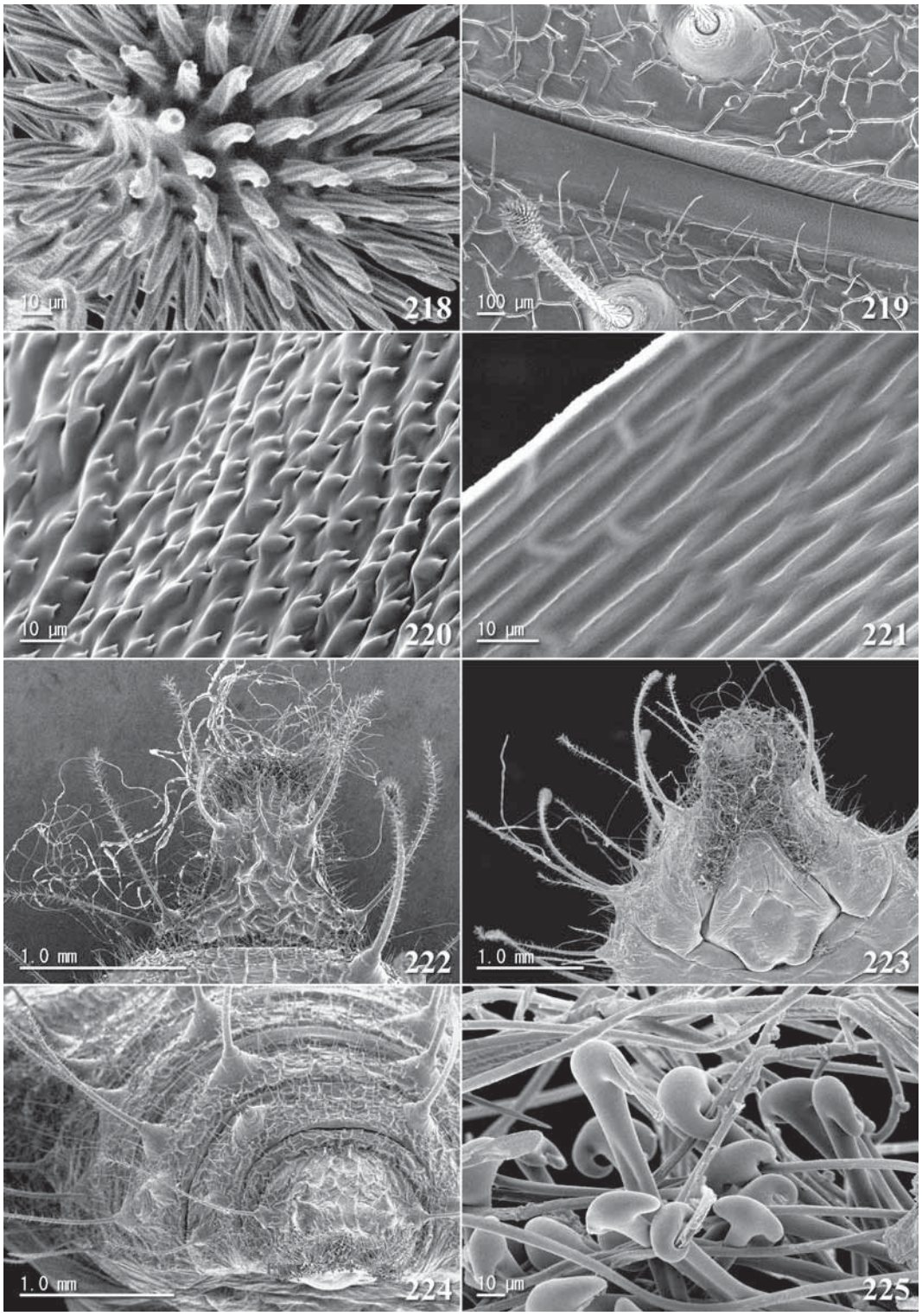
Surprisingly, host records of *E. procula* are from two different plant families, both in Costa Rica. One record is from a southwestern rainforest feeding on Myrtaceae (DeVries 1997) and the other from a northwestern rainforest feeding on Melastomataceae (Janzen & Hallwachs 2009).

Miconia-feeding *Euselasia* species as possible biological control agents of *Miconia calvescens*

The use of biological control agents for the management of invasive plant pests on tropical islands and other tropical habitats provides a viable alternative to traditional approaches of weed control and may represent one the least invasive and ecologically safe methods, especially when compared to the application of herbicides and other chemical treatmentss (Johnson & Denslow 2005; Denslow & Johnson 2006).



FIGURES 212–217. SEM of *Euselasia* pupa. **212)** Thoracic spiracle between T1 (right) and T2 (left), dorsal view (*E. chrysippe*); **213)** Surface sculpture of thoracic spiracle (*E. chrysippe*); **214)** Mesal portion of dorsum of T3–A1 showing silk-clipper structure (silken girdle *in situ*) on A1 (*E. bettina*); **215)** Cone-shaped raised base of clubbed setae; **216)** Stem of D-seta on left A6, dorso-lateral view (*E. chrysippe*); **217)** Apical area of D-seta on left A6, lateral view (*E. bettina*).



FIGURES 218–225. SEM of *Euselasia* pupa. **218)** Close-up of swollen tip of D-seta, dorsal view (*E. bettina*); **219)** Right subdorsal portion between A4 (bottom) and A5 (top), lateral view (*E. bettina*); **220)** Sculpturing of intersegmental membrane (tooth) on outer surface of lateral portion at right side posterior end of A5, lateral view (right = caudad) (*E. chrysippe*); **221)** Sculpturing of intersegmental membrane (cast) on inner surface of lateral portion on right side anterior end of A6, ventral to frontal view (top = caudad) (*E. chrysippe*); **222)** A8–10, cremaster and silk, dorsal view (*E. bettina*); **223)** A8–10, cremaster in 'V' shape, ventral view (*E. bettina*); **224)** A5–A10 caudal view (*E. bettina*); **225)** Cremaster, silk strands *in situ* (*E. bettina*).

FIGURES 226. Egg cluster of *Euselasia aurantia*, dorso-lateral view. Note the differences in color of eggs compared with *E. chrysippe* and *E. bettina*.

FIGURE 227. Egg cluster of *E. aurantia*, lateral view. Note space between eggs and plant surface.

Miconia-feeding *Euselasia* can be considered potential biological control agents for *Miconia calvescens* for the following reasons: 1) larvae are highly specific to their host plants as mentioned above (see also Table 1) and no native or economically important cultivated Melastomataceae are found in Hawaii. However, given the presence of commercial guava orchards (Hawaiian Alien Plant Studies 1998) and *Eucalyptus* plantations (Whitesell *et al.* 1992), host specificity tests using cultivated guava leaves (*Psidium guajava* L.), *Eucalyptus*, and other endemic myrtaceous plants (e.g. *Eugenia* spp. and *Metrosideros* spp.) is strongly recommended. This is because both Myrtaceae and Melastomataceae are in the order Myrtales; some species of *Euselasia* are known to feed on *Eugenia*, *Eucalyptus*, and *Psidium* (Table 1) and *E. procula* is reported to feed on both Melastomataceae and Myrtaceae. Moreover, the immature stages of *E. chrysippe* have been found only on melastomes through the massive caterpillar rearing project led by D. H. Janzen and W. Hallwachs over nearly 30 years (Janzen & Hallwachs 2009). 2) The larvae are gregarious feeders that devour leaf tissue in large quantities in relatively short periods of time, and their life cycle turnover is relatively short, approximately two months (this study; Allen 2007). However, the egg stage lasts relatively long compared to the larval and pupal stages and to the egg stage of other butterflies in general. According to Allen (2007), the egg stage lasted up to 6 weeks under field conditions at Reserva Ecológica Leonelo Oviedo. 3) They inhabit a wide range of elevations: *E. chrysippe* from sea level to 1500 m, *E. bettina* from 400 to 1250 m, and *E. aurantia* from 100 to 1700 m. 4) Adults feed on rotten fruit (under laboratory conditions; personal observation), extrafloral nectarines, and other non-floral sources (under natural conditions) (DeVries 1997). Also, the fact that females contain more than 160 eggs plus undeveloped immature eggs (this study) suggests that adults probably live for more than a month and that females oviposit more than once (Allen 2007). Another aspect of fruit-feeding is that it may function to keep adults alive and reproducing under laboratory conditions and in the field after release, i.e., they are not dependent on certain flowers for feeding.

Egg and egg stalk

The frustum-shaped eggs of the three *Miconia*-feeders documented in this study (*E. chrysippe*, *E. bettina*, and *E. aurantia*) are very similar in shape to those of the non-*Miconia*-feeders *E. mystica* and *E. hieronymi*, which feed on myrtaceous plants (Downey & Allyn 1980; DeVries 1997). In contrast, Hoffmann (1931) extracted 56 eggs from a reared female of *E. eucerus* and stated that the eggs are round with lines on the chorion.

The general coloration and pigmentation of eggs described appear to be relatively reliable for distinguishing species within the three *Miconia*-feeders. The eggs of *E. aurantia* (Figs. 226–227) can be distinguished from the other species studied herein by the following general characters: translucent pale-brown (slightly dull compared to *E. chrysippe*) with pigmentation of the apical rim area being purplish-faint black, extending close to one-half the egg height (becoming paler farther from the rim) along with dark lines extending from the lateral ridges. Several eggs lacked pigmentation except on the rim and lateral ridges, giving the impression that they are pale. Variation in the pigmentation within an egg cluster may not be uncommon, as observed in *E. chrysippe* and *E. aurantia*.

Stalked eggs were previously unreported in Lepidoptera. Thus far I have observed stalks on eggs of three species of *Euselasia* (i.e., *E. aurantia*, *E. bettina*, and *E. chrysippe*) but not on the eggs of *Corrachia leucoplaga* (Euselasiinae). Although the eggs of *E. hieronymi* (Downey & Allyn 1980) and *E. mystica* (DeVries 1997) were illustrated, stalks on the eggs were not documented. The function of the stalk is unknown apart from the fact that it keeps the eggs raised above the surface of the leaves.

The eggs of *Corrachia leucoplaga* are lozenge-shaped (i.e., short cylindrical), with a smooth surface; however, they resemble the eggs of *Euselasia* in the following: purplish pigmentation along the rim; lower bottom slightly wide, i.e. very slightly frustum shaped with round latero-ventral area; and concave micropyle area (n = 170 eggs; K. Nishida, in prep.). The stalk is absent (n = 167 eggs/cluster) and the stalk conjunctional structure apparently is absent (n = 3 eggs extracted from a female); i.e., it was not observed using the same 64X stereo-microscope that revealed the presence of the stalk and stalk conjunctional structure on the eggs of *Euselasia* species.

Harvey (1987b) and DeVries (1997) noted that the smooth barrel- to frustum-shaped eggs of Euselasiinae are unique within Riodinidae, and Lepidoptera in general, and that this character state potentially suggests a close relationship between *Styx*, *Corrachia*, and *Euselasia*. Hence, it is likely that stalked egg and stalk conjunctional structure is derived either within the genus *Euselasia* or the tribe Euselasiini. Furthermore, egg shape and pigmentation, and the biology of *Praetaxila segecia punctaria* (Fruhstorfer, 1904) in northern Australia and *Hamearis lucina* (Linnaeus, 1758) (Riodinidae: Nemeobiinae) in Europe are somewhat similar to those of *Euselasia*, although the eggs of the former species are laid in a loose cluster on the substrate (i.e., without stalks) (Harvey 1987b; Oates & Emmet 1990; Samson *et al.* 1999; Braby 2004; Kettner 2009).

General morphology of the larvae and pupae

The general appearance of the larvae and pupae of the two *Miconia*-feeding species, *E. chrysippe* and *E. bettina*, is similar, especially when compared to other *Euselasia* species that feed on other plant families (Hoffmann 1931; Brévignon 1997; DeVries 1997; Janzen & Hallwachs 2009). In fact, it is difficult to distinguish the larvae of *E. chrysippe* and *E. bettina* until they reach the last instar. Except for coloration and minor differences in body size, the two can be distinguished only by the form of the arrowhead setae. According to P.E. Allen (pers. comm. 2007), the mature last instar larva of *E. aurantia* is quite similar to that of *E. bettina*, and the overall appearance of the pupa is virtually identical to that of *E. chrysippe* and *E. bettina*. There are no significant differences in morphology and coloration that clearly separate the pupae of *E. chrysippe* and *E. bettina*.

Larval morphology

A detailed examination of the larvae of *Euselasia chrysippe* and *E. bettina* revealed many morphological features previously unrecorded in lepidopteran larvae, particularly in the first instar. In many Lepidoptera the first instar shows specialized behaviors which often are related to establishment on the host plant (Zalucki *et*

al. 2002). Hence, further studies are required to determine the possible functions of the circular tablet organs, the bladelike setae, the flat setae, the large number of setae in most of the setal groups (in contrast to the absence or reduction in the number of setae in some groups), and the bifurcate D-group setae, which occur only in first instar larvae.

Bifurcate dorsal setae are reported in exceedingly few Lepidoptera. They were observed in the first instar of *Praetaxila segecia punctaria* (Samson *et al.* 1999), potentially representing a synapomorphy for *Praetaxila* and *Euselasia*. However, because the first instars of so few other riodinids have been reported, the taxonomic distribution of this character state is poorly known. Extraordinarily, the dorsal setae of first instar larvae of some species of *Catasticta* group (Pieridae: Pierinae) are bifurcated at the apex (Braby and Nishida, in press).

Differences in the shapes of PCOs (sunken, flat, or raised) and spherical organs (flat to papillalike) may be artifacts of larval preservation or in preparation for SEMs. It is also uncertain whether the sphere part of the spherical organ and/or the raised part of the PCO are part of the secretion or part of the organ itself.

Other major differences between the first instar and other instars of these two *Euselasia* species are the location of the circular tablet organ and spherical organ on the T1 shield, as well as the large, stout bladelike seta on each T1 leg. The functions and homologies of these features among different instars and among other species are unknown. The conclusion that lateral fusion has occurred in A8 and A9 was determined by external appearance, not by dissections to observe internal muscle attachment.

The complement of setae on the anal plate is unusual, exceeding the numbers seen in other setal groups on other segments (N. Kristensen and I. Hasenfuss, pers. comm. 2006). However, the naming of the setae was avoided because their homologies with other setae remain unknown.

Feeding mode and mandibular morphology

The mandibles of first and second instars possess sharply pointed, distinct teeth, the tips of which overlap slightly, allowing shearing of leaf tissue. Larvae of these instars feed by grazing on the surface tissue of the leaf. Considerable change in mandible morphology occurs between the second and third instars, and there is a concomitant change in the feeding mode from grazing (in the second instar) to grazing, skeletonizing, and feeding on entire leaf tissue, including the thin veins (in the third instar). The mandibles in the third instar possess less distinct teeth with a concave inner surface, possibly allowing them to feed both by grazing the surface (as in earlier instars) and clipping through entire leaf tissue (as in later instars). The single sharp ridgelike teeth with a more deeply concave inner surface of later instars likely allow larvae to bite through the entire leaf tissue. Changes in feeding modes and mandibular morphology also have been observed in the larvae of the leaf-tying moth *Psilocorsis cryptolechiella* (Chamber, 1872) (Oecophoridae) on *Fagus grandifolia* Ehrh. (Fagaceae) (Embree 1958 [cited as *P. gaginella*]) and in external-feeding *Heterocampa obliqua* (Packard, 1864) (Notodontidae) on *Quercus macrocarpa* Michx. (Fagaceae) (Godfrey *et al.* 1989). Godfrey *et al.* (1989) hypothesized that loss of the sharply pointed mandibular teeth in these two species is related to the change in feeding mode from grazing on leaf surface tissue to clipping the entire leaf tissue. This observation in *Euselasia* may represent the first documented case of changing mandibular morphology associated with feeding mode in butterflies.

Structural color plates

High magnification SEM images (up to 41,000X) of cuticle surface of the structural color plates did not reveal any micro-structures that might produce iridescence. Even under this magnification, the surface was smooth. It is possible that such structures were modified or destroyed in the process of SEM specimen preparation. The structural color plate of larvae boiled in water and preserved in 75% EtOH did not show a metallic-blue iridescence as is obvious in live specimens (Fig. 195). None of the larvae treated with 100% EtOH and critical point dried showed any of the metallic color. However, dry-preserved molted skins of both species had dark purplish shiny iridescence. When the skins were soaked in water, the iridescence on the structural color plate became pale metallic-purple to pale-blue. It is likely is that the structure is internal, i.e., located below the cuticular surface in multiple semi-translucent layers. Thus, it may be necessary to dissect the structural color plate and use SEM or use transmission electron microscope to reveal its structure (M. Hoshi, pers. comm. 2006).

Structural colors are uncommon in larvae of Lepidoptera, and presumably they function in aposematism. There are several examples of aposematism in gregarious larvae of other Lepidoptera (e.g., S.-Tullberg & Hunter 1996), but bright coloration obviously is not restricted to gregarious species. Solitary last instar larvae of some *Melese* and *Bertholdia* species (Arctiidae) have rows of bright metallic-blue spots on the dorsum (pers. obs. 2007). Last instar larvae of *Doleschallia bisaltide* (Cramer, 1777), *D. dascylus* Godman & Salvin, 1880, *D. noorna* Grose-Smith & Kirby, 1893, *Yoma sabina* (Cramer, 1780) (Nymphalidae: Nymphalinae) exhibit metallic-blue on the basal area of their dorsal to lateral setae (Igarashi & Fukuda 1997, 2000), and several species of saturniids have silver markings on their dorsum: e.g., *Actias dubernardi* (Oberth.) (Ylla *et al.* 2005); *Sphingicampa hubbardi* (Dyar) (Sawby 2005); *Syssphinx* species (Janzen & Hallwachs 2009); and some African saturniids (R. Peigler, pers. comm. 2006).

Number of larval instars

In the family Riodinidae, it is not unusual for larvae to have more than five instars (D.J. Harvey, pers. comm. 2006). For example, *Lemonias caliginea* (Butler, 1867) [cited as *Anatole rossi*] has six (Ross 1964), and *Calephelis borealis* (Grote & Robinson, 1866) (dos Passos 1936) and *C. muticum* McAlpine, 1937 (McAlpine 1938) have eight to nine instars; all are members of Riodininae. Zanuncio *et al.* (1990, 1995) reported that the larvae of *Euselasia hygenius* on *Eucalyptus urophylla* S. T. Blake has six instars and that *Euselasia melaphaea* [cited as *E. apisaon*], *E. eucerus*, and *E. hygenius occulta* have five instars. It should be noted that *E. hygenius occulta*, or *E. occulta* Stichel, 1919 is a synonym of *E. hygenius*, according to Callaghan & Lamas (2004). According to Chacón (2001), *E. chrysippe* has five larval instars. Although there appear to be differences in the number of instars, the presence of six instars in *Euselasia* is apparently common. The number of larval instar in related genera and tribes is not available. Furthermore, *Hamearis lucina* and *Praetaxila segecia punctaria* (Nemeobiinae) have four (Oates & Emmet 1990) and five (Samson *et al.* 1999) instars, respectively. It is noteworthy that mis-counting of instars frequently occurs during the rearing of middle instars owing to their extreme similarity and rapid development (pers. obs.; P.E. Allen, pers. comm. 2007).

Processionary behavior

The processionary behavior of the larvae is facilitated, at least in part, by tactile stimuli (contacts made by setae) and an extra-silk chemical substance(s) which functions as a trail pheromone. The tactile stimuli appear to take priority over the chemical marker and silk as shown in other processionary lepidopteran species (Fitzgerald & Pescador-Rubio 2002; Fitzgerald 2003). However, no experiments were conducted to determine if silk laid during the procession serves any function beyond allowing larvae to grip the substrate during locomotion. Halting and reinitiating the procession are most likely controlled by setal contact of the larva with those in front and behind. Although the origin of the trail pheromone is unknown, the following two organs are possible sources or disseminators of it: 1) the claw-shaped setae on the venter of A10 between the prolegs (Figs. 130, 134–135, 145, 206–207), and 2) mesally located spatulate-tipped setae on the thoracic legs (Figs. 111, 115, 176–181). These are the only organs that are present in all larval instars and appear to make consistent contact with the substrate. Larvae dragged the tip of the last abdominal segment on the substrate while moving in procession (Fig. 43; Nishida 2007), suggesting that setae here, perhaps including the cuticle, might be the pheromone source. The same type of dragging behavior has been observed in several other processionary lepidopteran caterpillars, for example *Hylesia lineata* Druce (Saturniidae), *Gloveria*, and *Malacosoma* (Lasiocampidae) (Fitzgerald 2003, and references therein). In addition, Fitzgerald & Pescador-Rubio (2002) observed 'specialized' setae on the ventral surface of the tip of the last abdominal segment (i.e., located in a position similar to that in *Euselasia*) on *Hylesia lineata* larvae that are morphologically unique and suggested that these setae are the most likely source of the trail pheromone.

With regard to the second possible source, the spatula-shaped setal tips are appropriate for spreading a substance and they make contact with the substrate during locomotion. In Riodinidae, these setae are known only in Euselasiinae and are considered to be a synapomorphy for the subfamily. This character state has not been reported in any other butterfly species (Harvey 1987b; D.J. Harvey, pers. comm. 2006). Furthermore, all

known euselasiine larvae are gregarious, and possibly all exhibit processionary behavior (see references in Table 1). It should also be noted that the larvae of *Praetaxila segecia punctaria*, and *Abisara kausambi* C. & R. Felder, 1860 (Nemeobiinae) in the Old World, exhibit gregarious habit (Samson *et al.* 1999, Igarashi & Fukuda 2000) and most likely are processionary.

Laboratory mixtures of larvae in different instars and of *E. chrysippe* and *E. bettina* suggest that the trail pheromone is probably similar in composition between instars and between these two species. The observation that larvae react to touch with a fine brush suggests that the tactile stimuli are not species specific.

Jörgensen (1932) reported that small groups of larvae of *Euselasia eugeon* (Hewitson, 1856) were found inside a silk structure on *Chrysophyllum cuneifolium* (Rudge) A. DC. (Sapotaceae). If the silk structure was constructed by the larvae, it will be worth investigating because this behavior appears to be absent in *E. chrysippe* and *E. bettina*.

Possible function the SD2 sensitive setae and retracting and flicking of the head

The results of the setal removal experiment suggest that the receipt of air-borne vibrations is related to the retracting of the head and 'pulsed-head flicking' behavior. The SD2 seta on the T1 shield is the only seta which is socketed loosely on the pinaculum; thus it is likely to be the most sensitive to air movement (D.J. Harvey, pers. comm. 2006). With slight air movement, only the SD2 seta waved like a feather from the basal socket in a maximum angle of 15 to 20° (personal observation). The basal part of the seta and the movement appear to be similar to that of *Barathra brassicae* L. (Noctuidae) in which the seta is located on the dorsum of T1 (Markl & Tautz 1975; Tautz 1977). Tautz & Markl (1978) observed that *B. brassicae* reacted to airborne vibrations of an approaching wasp, *Dolichovespula media* (Retzius) (Vespidae), by contraction of the thoracic segments and squirming and dropping from the leaf. However, after removal of the 'sensitive setae' (referred to as sensory hairs), the larvae no longer reacted to the vibrations. In their experiment, 'hairless' larvae had a significantly higher rate of attack by the vespid wasp than larvae with an intact seta ($P < 0.001$), and they concluded that the 'hearing' capacity of the larva can function as a defense against predatory or parasitoid wasps or flies. The retracting of the head and 'pulsed-head flicking' in the larvae of *E. chrysippe* and *E. bettina* probably also has a defensive function against predators or parasitoids.

Loosely socketed setae located in a similar position on the T1 shield have been documented by Ballmer & Pratt (1988) (referred to as sensory setae) in 23 species of Lycaenidae in five subfamilies and in two species of Riodinidae, *Zemeros flegyas* (Guerin, 1843), and *Melanis pixe* (Boisduval, 1836). Similar setae also have been found in other lycaenid genera, e.g., *Calospila*, *Erora*, *Stymon* (D. J. Harvey, unpublished), and *Calycopsis* (Duarte *et al.* 2005, labeled as SD1); and in other riodinid genera, e.g., *Calephiles*, *Eurybia* (D. J. Harvey, unpublished), and *Juditha* (Hall & Harvey 2001). Setae homologous with the loosely socketed setae also were reported from all segments in Nymphalidae (Harvey 1991). This type of seta has not been observed in endophagous larvae (D.R. Davis & D. Adamski, pers. comm. 2007).

Miller *et al.* (2006) noted that the penultimate instar larvae of *Hylesia lineata* raise their head and the front half of the body in response to human vocalization, which may be similar to their response to tachinid wing buzzing. Braby & Nishida (2010) observed that the rapid and frequent raising of the head and anterior body in late instar *Pereute charops* (Boisduval, 1836) and *P. cheops* (Staudinger, 1884) (Pieridae: Pierinae) drove away some chalcidid wasps and a tachinid fly. It is also noteworthy that some lepidopteran larvae are known to detect substrate-borne vibrations (Yack *et al.* 2001) as may be the situation in *E. chrysippe* and *E. bettina*.

Pupation site and 'tooth-cast' system of pupal abdominal segments

The pupation site in the field was away from the host plants but still remains unknown. Under captive conditions, the larvae pupated gregariously or singly on the underside of surrounding objects, so in nature they may occur on underside of leaves, branches, or on trunks, etc. where they are protected from direct sunlight and rainfall. Larvae of *Euselasia melaphaea* pupate on the underside of leaves and on trunks of host trees (Zanuncio *et al.* 1990 [cited as *E. apisaon*]). A solitary pupa of *E. procula* was found on the adaxial surface of a leaf of *Eugenia* sp. (DeVries 1997; P. DeVries, pers. comm. 2004). Miller *et al.* (2006) note that the larvae of *E. eubule* pupate singly on leaves near the host plant. Hoffmann (1931) briefly notes that the larvae of *E. eucerus* pupate together.

The two *Euselasia* species in this study both possessed a 'tooth-cast' system of spinelike sculpturing in the intersegmental membrane on the outer surface of the lateral portion at the anterior edge of segments A5–7 (Fig. 220) and a complementary transversely ridged sculpturing on the inner surface of the lateral portion of the intersegmental membrane at the posterior edge of segments A4–A6 (Fig. 221). The 'tooth-cast' system of the two *Euselasia* species does not appear to be involved in sound production. However, no precise measurements were taken to evaluate very high or very low frequencies or substrate borne sounds potentially produced by *Eusleasia*. In lycaenids Downey & Allyn (1973) also concluded that these structures are not involved in producing stridulatory sounds that function for protection or defense.

It is interesting to note that Downey & Allyn (1973) observed the 'tooth-cast' sysetm between abdominal segments 4 and 5 and between 5 and 6 in lycaenids but did not find similar structures in the riodinid species they studied (all in the subfamily Riodininae). Hence, it is possible that these structures are restricted to Euselasiinae in Riodinidae; however, the taxonomic distribution of the feature is too poorly known to draw such conclusions.

Adult eclosion and flight hours

Females of *E. chrysippe* and *E. bettina* always eclosed before males. This is consistent with observations by Brévignon (1997) for *E. thusnelda* and *E. euryone*. The later eclosion of males in the two *Euselasia* species in this study, combined with the findings of Brévignon (1997), suggest that inbreeding in *Euselasia* most likely occurs in very low frequency. However, according to Miller *et al.* (2006) males typically eclose one day before females in Riodinidae; they indicate that males of *E. eucerus* (Hoffmann 1931) eclosed prior to the females, but males and females of *E. eubule* eclosed on the same day.

In the field, adults of *E. bettina* were observed more commonly than those of *E. chrysippe*, contrary to observations of the immature stages. The flight activity of *E. chrysippe* was very early (starting between 0630 and 0730 hr) and short compared to other butterflies in general. This early and short period of daily activity could possibly explain why they were observed less frequently than *E. bettina* which has a daily activity pattern slightly later (between 0730 and 0900 hr). DeVries (1997) described flight activities of both *E. chrysippe* and *E. bettina*; he recorded flight hours for *E. bettina* similar to those reported above, but for *E. chrysippe* different from those reported above.

Parasitoids

Eggs of both *Euselasia chrysippe* and *E. bettina* were parasitized by *Encarsia* cf. *porteri*. *E. porteri* is a common species in the Neotropics and is known to have an interesting biology in which females develop in completely different sets of hosts than males (Polaszek & Hanson 2006). Males develop principally in eggs of Lepidoptera and the females in whiteflies (Hemiptera: Aleyrodidae). All *Encarsia* reared in the present study were males. Unfortunately, there have been introductions of *Encarsia* species in Hawaii to control whiteflies (e.g., Heu 2002–2004). It seems that *E. porteri* has not been introduced to Hawaii since the species is not listed among the 17 species of *Encarsia* recorded in Hawaii (Bishop Museum 2002).

Another egg parasitoid reported from *Euselasia* is *Trichogramma maxacalii* Voegele & Pointel (Trichogrammatidae) in eggs of *Euselasia apisaon* feeding on *Eucalyptus* in Sao Paulo and Minas Gerais, Brazil (Oliveria *et al.* 2000). This parasitoid also is absent from the list of the Bishop Museum (2002). Janzen & Hallwachs (2009) provide data on parasitoids reared from some *Euselasia* species which is summarized in Table 2. With regard to *Calolydella* sp. (Tachinidae) reared from *Euselasia chrysippe* in this study, it probably is not host-specific, as several species of *Calolydella* have been reared from various families of Macrolepidoptera and from an argid sawfly (Janzen & Hallwachs 2009).

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